Guide to the Parasites of Fishes of Canada

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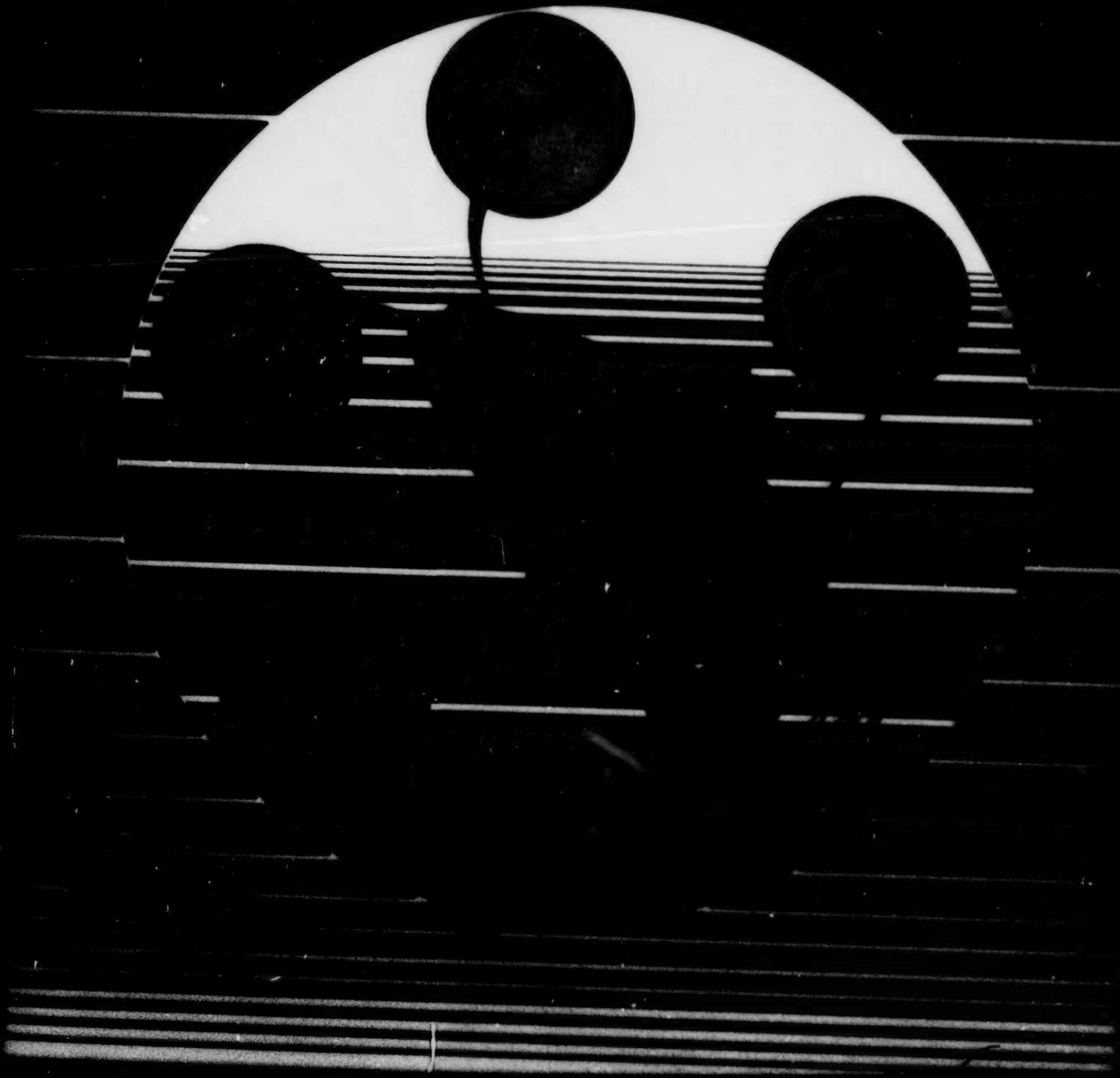

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GUIDE TO THE PARASITES OF FISHES OF CANADA

PART I

Entobdella hippoglossi (O. F. Muller, 1776) Johnston, 1856 (Dactylogyrida: Capsalidae) from the body surface of the Pacific halibut, *Hippoglossus stenolepis* Schmidt, 1904, taken in coastal waters of British Columbia. (Ventral view.)

Canadian Special Publication of Fisheries and Aquatic Sciences 74

Guide to the Parasites of Fishes of Canada

Edited by L. Margolis and Z. Kabata

Part I

General Introduction

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Monogenea and Turbellaria

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GENERAL INTRODUCTION

L. MARGOLIS AND Z. KABATA

In 1978, Margolis and Arthur (1979) completed their "*Synopsis of the parasites of fishes of Canada*", which was intended to serve as a stepping stone towards the realization of a longer range goal of preparing an illustrated "Guide to the parasites of fishes of Canada". The account of the Monogenea and Turbellaria, which this introduction precedes, represents the first phase in the achievement of that goal.

The need for a compendium allowing for relatively easy identification of the parasites of fishes of Canada has long been recognized by the editors. Current trends in biological education have been instrumental in producing a generation of workers well equipped for dealing with the intricacies of intracellular events or with the large-scale events in community ecology and population biology, but often handicapped when faced with identifying unknown organisms. The information explosion of recent decades has made specialization inevitable and deprived many biologists of the opportunity of becoming better acquainted with the broad range of animal groups contributing to the parasite fauna of fishes. Nevertheless, precise knowledge of the identity of a species of fish parasite is crucial to the success of certain types of biological research concerning fish and fisheries. Both marine and freshwater fish have come to occupy centre stage in many types of ecological drama, played against the background of popular concerns. Environmental pollution and the problems it has generated often involve fish, either as victims or as indicator organisms. To understand the nature of the impact various factors exert on fish, one must take into consideration and evaluate the influence of parasites on the well-being of the host. Studies of evolution and phylogeny of fishes and the practical aspects of fish stock identification and migrations have also involved, with increased frequency, parasites as clues to these complex and still poorly understood processes and events. In these and other instances the identities of the parasite species must be known with certainty, if erroneous conclusions are to be avoided.

Based on the views expressed above, it is expected that the various parts of this "Guide" will find use not only among fish parasitologists, but also among fisheries scientists and biologists, ecologists, aquaculturists, fish health inspectors and diagnosticians, and technologists concerned with fish quality inspection.

In embarking on this project we are cognizant of the fact that the faunal information on which it is based is incomplete. Future studies will undoubtedly increase the number of parasite species known to be associated with Canadian fishes and will add further data on geographic and host distribution of the parasites. Nevertheless, the available data base is sufficiently extensive to warrant the present undertaking, which can be revised as circumstances demand in future years.

The existing parasitological literature offers few examples of compendia such as that envisaged by the present editors. Perhaps the best known among them is the *Key to the parasites of the freshwater fishes of the U.S.S.R.*, a publication by a team of Soviet parasitologists, who, with their customary industry put together keys to species of all groups of parasites of their freshwater fishes in a single, 776-page volume (Bykhovskaya-Pavlovskaya et al. 1962). Subsequently translated into English, this book is an expanded, illustrated set of keys, accompanied by brief introductory notes on each group. The English language literature contains the well-known *Parasites of North American freshwater fishes* by G. L. Hoffman (1967), which provides keys and/or definitions of taxa down to the generic level, each genus being accompanied by a list of its species. There are also English language publications that offer diagnoses and keys to particular groups of parasites from all fishes (marine and freshwater) from a limited geographic area. An example is Kabata's (1979) *Parasitic Copepoda of British fishes*. However, to our knowledge, no publication currently exists that encompasses keys to all the parasite groups of all fishes in any country that has both a freshwater and marine fauna.

With these precedents and the needs of a variety of Canadian biologists in mind, the editors took the initiative of inviting a team of Canadian specialists, each with expert knowledge of a particular group of parasites, to collaborate on writing and publishing this series. The guiding principle for the format decided upon was the ease of identification of the species within each group of parasites. The basic style chosen was, therefore, a key, in an expanded form. We envisioned that each supraspecific taxon would be preceded by a brief diagnosis, with explanatory diagrams if necessary. Such diagnoses were to be followed by a key to taxa of the next lower rank. The keys to species were to include brief diagnoses of all species, to which other pertinent information was to be added, such as the host list and distribution in Canada accompanied by appropriate references. Only Canadian records were to be considered, unless there were valid reasons to include others. Where appropriate, cues to identifying features, contained in each couplet of the key, were to be illustrated by drawings, with references to figures being placed directly in the keys. The basis for the species inventory, hosts, and geographical records is the publication by Margolis and Arthur (1979), which summed up all relevant published information to the end of 1977. Subsequently published discoveries and individual author's own unpublished records would, of course, also be included.

It was the editors' original intention to publish the entire work in a single volume. This plan, however, could not be realized. It proved impossible to put together a team of contributors who could assure completion of these tasks synchronously. Consequently, there was no possibility of receiving all contributions within a specified time frame to enable publishing them all together. Taking into account also the fact that keys of this type require periodic updating to include the results of new studies that expand our faunal data base, and that keys to different groups age at different rates, we decided to opt for publication, under a common title, of a series of separate issues. Each issue will deal with a different group of parasites, or, as necessary, with several small groups together. The present plans envisage publication of keys to the following taxa: Protozoa, Turbellaria, Monogenea, Trematoda, Cestoda, Acanthocephala, Nematoda, Hirudinea, Mollusca, Crustacea (Copepoda, Isopoda, Amphipoda, and Branchiura), Acarina, and Cnidaria.

It would be desirable, of course, to maintain a uniform format within the series. However, in view of some necessary differences in treatment required by different groups of parasites, and in view of personal preferences of the individual authors, slight differences of format will be present among the parts in the series. Equally, differences in treatment and labelling of figures can be expected. They will not be serious or extensive enough to disrupt the unity of the series.

In presenting the first part of the "Guide" to the biological community of Canada, the editors hope that this part, and the entire series, will become a ready reference and a useful tool for all those concerned with identification of fish parasites. Feedback from users of the "Guide" will always be appreciated.

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MONOGENEA AND TURBELLARIA

MARY BEVERLEY-BURTON

ABSTRACT

Beverley-Burton, M. 1984. Monogenea and Turbellaria, p. 5–209. *In* L. Margolis and Z. Kabata [ed.] Guide to the parasites of fishes of Canada. Part I. Can. Spec. Publ. Fish. Aquat. Sci. 74: 209 p.

The present issue contains keys, diagnoses, morphometric data, figures and records (updated from Margolis and Arthur 1979 to the end of 1983) for the 183 species of Monogenea and Turbellaria known from fishes of Canada. The keys to Monogenea are under three major taxa of equal status, arbitrarily designated as orders: Dactylogyrida, Gyrodactylida, and Polyopisthocotylida. The family Microbothriidae is not assigned to a higher taxon and *Udonella* is included in the Turbellaria. The following new taxonomic proposals are made (listed in order of appearance in text): Ancyrocephalidae — *Actinocleidus scapularis* Mizelle and Donahue, 1944 and *A. sigmoideus* Mizelle and Donahue, 1944 synonyms of *A. incus* Mizelle and Donahue, 1944; ***Ligictaluridus*** n. g. with *L. pricei* (Mueller, 1936) n. comb. (type species) and *L. floridanus* (Mueller, 1936) n. comb.; *Urocleidus procax* Mizelle and Donahue, 1944 synonym of *Onchocleidus similis* Mueller, 1936, *O. chrysops* (Mizelle and Klucka, 1953) n. comb., *O. attenuatus* (Mizelle, 1941) n. comb., *O. rogersi* (Hanek and Fernando, 1972) n. comb.; ***Salsuginus*** n. g. with *S. angularis* (Mueller, 1934) n. comb. (type species) and *S. fundulus* (Mizelle, 1940) n. comb.; *Tetracleidus stentor* (Mueller, 1937) n. comb., *T. capax* (Mizelle, 1936) n. comb., *T. glenorensis* (Hanek and Fernando, 1972) n. comb., *Cleidodiscus uniformis* (Mizelle, 1936) synonym of *T. longus* (Mizelle, 1936) n. comb.; *Urocleidus baldwini* (Dechtiar, 1974) n. comb.; Pseudomurraytrematidae — *Pseudomurraytrema muelleri* Price, 1967 synonym of *P. alabarrum* Rogers, 1966; Gyrodactylidae — *Gyrodactylus lairdi* Hanek and Threlfall, 1969, *G. memorialis* Hanek and Threlfall, 1969 and *G. terranovae* Hanek and Threlfall, 1969 synonyms of *G. avalonia* Hanek and Threlfall, 1969.

Four appendices provide (1) a classification of the organisms covered, (2) a synoptic version of the evolution of the major monogenean taxa found on fishes of Canada, (3) notes on the systematic status of *Udonella* and Microbothriidae, and (4) diagrams and a discussion of North American ancyrocephalid "penis" types.

RÉSUMÉ

Beverley-Burton, M. 1984. Monogenea and Turbellaria, p. 5–209. *In* L. Margolis and Z. Kabata [ed.] Guide to the parasites of fishes of Canada. Part I. Can. Spec. Publ. Fish. Aquat. Sci. 74: 209 p.

Le présent volume contient les clés, les diagnoses, les données morphométriques, les figures et les spécimens signalés (mis à jour de Margolis et Arthur 1979 jusqu'à la fin de 1983) pour 183 espèces de Monogenea et de Turbellaria, parasites du poisson au Canada. Pour les Monogenea, les clés sont classées selon trois principaux taxons de statut égal, désignés arbitrairement comme ordres: Dactylogyrida, Gyrodactylida et Polyopisthocotylida. La famille Microbothriidae n'est pas classifiée dans un taxon supérieur et *Udonella* est incluse dans les Turbellaria. On fait les nouvelles propositions taxonomiques suivantes (selon l'ordre de présentation dans le texte): Ancyrocephalidae — *Actinocleidus scapularis* Mizelle et Donahue, 1944 et *A. sigmoideus* Mizelle et Donahue, 1944 comme synonymes de *A. incus* Mizelle et Donahue, 1944; ***Ligictaluridus*** n. g. avec *L. pricei* (Mueller, 1936) n. comb. (espèce-type) et *L. floridanus* (Mueller, 1936) n. comb.; *Urocleidus procax* Mizelle et Donahue, 1944 comme synonyme de *Onchocleidus similis* Mueller, 1936, *O. chrysops* (Mizelle et Klucka, 1953) n. comb., *O. attenuatus* (Mizelle, 1941) n. comb., *O. rogersi* (Hanek et Fernando, 1972) n. comb.; ***Salsuginus*** n. g. avec *S. angularis* (Mueller, 1934) n. comb. (espèce-type) et *S. fundulus* (Mizelle, 1940) n. comb.; *Tetracleidus stentor* (Mueller, 1937) n. comb., *T. capax* (Mizelle, 1936) n. comb., *T. glenorensis* (Hanek et Fernando, 1972) n. comb., *Cleidodiscus uniformis* (Mizelle, 1936) comme synonyme de *T. longus* (Mizelle, 1936) n. comb.; *Urocleidus baldwini* (Dechtiar, 1974) n. comb.; Pseudomurraytrematidae — *Pseudomurraytrema muelleri* Price, 1967 comme synonyme de *P. alabarrum* Rogers, 1966; Gyrodactylidae — *Gyrodactylus lairdi* Hanek et Threlfall, 1969, *G. memorialis* Hanek et Threlfall, 1969 et *G. terranovae* Hanek et Threlfall, 1969 comme synonymes de *G. avalonia* Hanek et Threlfall, 1969.

Les quatre appendices contiennent (1) une classification des organismes étudiés, (2) une version synoptique de l'évolution des taxons principaux de Monogenea qui parasitent les poissons au Canada, (3) des notes sur le statut taxonomique de *Udonella* et de la famille Microbothriidae et (4) des diagrammes et une discussion des types de «pénis» trouvés dans la famille Ancyrocephalidae en Amérique du Nord.

INTRODUCTION

The appearance of the *Synopsis of the parasites of fishes of Canada* by Margolis and Arthur in 1979 represented a landmark in Canadian parasitology. The projected publication of keys for the major taxa parasitizing fishes will, hopefully, facilitate the identification of the parasites and also identify the relevant taxonomic papers. In the present work, which covers the parasitic Turbellaria and the Monogenea, it was necessary to consult nearly 300 references, some of which are from obscure journals.

The present volume contains keys, diagnoses, morphometric data, figures, and records (updated from Margolis and Arthur 1979 to include papers published before the end of 1983 and my own more recent publications) for both hosts and geographic localities. Where possible, observations, by myself or my co-workers, on material in my own collection or borrowed type specimens are used to supplement published data, but it was impossible to restudy the entire spectrum of monogenean parasites which have been found in Canada. Thus, it is necessary to point out that some of the keys, separating poorly described species, are less than satisfactory. Host specificity has been used extensively in separating species. In many cases this is legitimate as monogeneans are often highly host specific. Nevertheless, in genera such as *Dactylogyrus*, where there is a paucity of morphological and morphometric criteria, it is evident that host specificity is overemphasized. A work such as this can only be as good as the available data. Nevertheless, a start has been made, and it is expected that these keys will provide a stimulus for future observations and continual revision.

A major difficulty I encountered was to decide on a scheme of classification (Appendix 1) enabling me to present the material systematically. The taxonomy of the phylum Platyhelminthes has been a source of controversy for many years and remains a topic of considerable zoological interest. Therefore, I reviewed some of the ideas presented by recent authors who have examined the relationships of the major taxa within the Monogenea (e.g. Bykhovsky 1957; Baer and Euzet 1961; Yamaguti 1963; Llewellyn 1970; Lambert 1979; and Malmberg 1982) and have considered several different viewpoints. As a pragmatic approach I decided that, rather than enter into some of these controversial issues, I would adopt (with a few cautious modifications) the scheme described by Llewellyn (1970). A synopsis of Llewellyn's paper is given in Appendix 2 to provide the rationale for both the classification and the keys to the major taxa. I have only included taxa which have representatives recorded as parasites of fishes taken in Canada; thus Appendices 1 and 2 are presented with an awareness of the Canadian fauna and are not intended to apply in a "global" context.

Having selected an overall scheme of classification, it became obvious that comment and systematic revision were necessary for some taxa. Rather than include taxonomic discussions in the text, they are presented in Appendix 3 and new systematic proposals are listed in the summary.

The material in the present work consists of: keys to the various taxa of Turbellaria and Monogenea parasitizing fishes of Canada, the Host-Parasite list, Acknowledgements, References, Appendices, Indices, and Summary.

The monogenean *KEYS* are under three major groups of equal status, arbitrarily designated as orders: Dactylogyrida, Gyrodactylida, and Polyopisthocotylida. The family Microbothriidae Price, 1936 is not assigned to a higher taxon as its affinities are far from clear and *Udonella* (following Ivanov and Mamkaev 1973) is included in the Turbellaria.

Families and genera are treated alphabetically once they have been "keyed out", and diagnoses are included for these taxa. Data concerning each species are incorporated into the keys and/or tables, and the following information is provided using, with minor modifications, the format of Margolis and Arthur (1979):

1. The current *scientific name* including author(s) and date(s).
2. Reference to the appropriate *figures* (arranged alphabetically) and *tables of comparative morphometric data**. Measurements, unless otherwise stated are presented in micrometres (μm). Where possible, the range, or the mean with range in parentheses, is given.
3. *Synonyms* which have been proposed since the publication of Margolis and Arthur (1979), or are proposed for the first time within the present work.
4. The *site(s)* or location(s) of occurrence of the parasite on its host(s). When the site was not given in the Canadian records, the likely site, as determined from the literature, is enclosed in square brackets.
5. The *host(s)* are cited using currently accepted scientific names. Names preceded by a question mark (?) represent questionable records. Numbers in parentheses after each host name

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*In some instances these have been incorporated into the keys.

correspond with the numbers assigned to the references from which the parasite-host records were established.

6. *Records* — the authors responsible for the *records* are listed in chronological order of the published records. To enable the reader to grasp at a glance the author(s) responsible for particular parasite-host-locality records, I numbered the references listed under "Records" and placed the corresponding number(s) after the host name, and each reference is followed by the locality or localities from which the parasite was reported. When only one host is listed for a particular parasite the references are not numbered.
7. *Geographic locality(ies) — Distribution* within Canadian waters. Marine species are grouped into two geographic regions: Atlantic (Atl), and Pacific (Pac). Freshwater distribution is indicated by provincial or territorial boundaries listed in alphabetical order as follows: Alta (Alberta), BC (British Columbia), Lab (Labrador), Man (Manitoba), NB (New Brunswick), Nfld (insular Newfoundland), NS (Nova Scotia), NWT (Northwest Territories), Ont (Ontario), PEI (Prince Edward Island), Que (Quebec), Sask (Saskatchewan), and YT (Yukon Territory). For reports from anadromous and euryhaline fishes taken in brackish or estuarine waters, the abbreviation of the geographical locality is followed by "b", e.g. BC-b, indicating British Columbia, brackish waters. In some cases, such as several papers by Margolis, where the records are known to be estuarine, but are not so indicated in the original paper, they are nevertheless listed here with a "b".
8. *Remarks* are offered on systematics, nomenclature, and other items where confusion is known to occur in the literature.
9. *Footnotes* are used for explanatory notes.

Selected FIGURES representative of the major taxa, are labelled to clarify the typical internal anatomy of each group.

The HOST-PARASITE list is organized according to the phylogenetic relationships of major host taxa as given by Robins et al. (1980) for North American fishes.

Within each family, genera and species are listed alphabetically. The scientific and common names of fishes are those recommended in Robins et al. (1980), except when these names have not been accepted by Hart (1973) for Pacific fishes or by Scott and Crossman (1973) for freshwater fishes; in these cases the names recommended by the latter authors are used. Host synonyms are not included. After the name of each parasite species, its geographic distribution on/in the host in question is given in parentheses. A single asterisk (*) after the parasite name indicates a tentative, provisional, or presumptive original parasite identification, or indicates that a subsequent worker has tentatively referred a previous record to the indicated species. A double asterisk (**) after the parasite name indicates that the original or a subsequent author has considered the parasite to be of abnormal occurrence (i.e. a pseudoparasite or accidental parasite) for the host in question. An interrogation mark (?) preceding a parasite name indicates questionable validity of the parasite identification and the same mark after a locality citation indicates an ambiguous or uncertain locality record.

The REFERENCES are listed alphabetically and are all directly referred to in the text. An INDEX is provided for the parasites and the hosts listed alphabetically by their scientific names. The SUMMARY contains a synoptic list of taxonomic proposals.

Appendix 3 contains notes on the systematic positions of *Udonella* and the Microbothriidae.

Appendix 4 (with its Fig. 1-7) is a synoptic account of the distinct "penis" types which I recognize among the ancyrocephalid genera found on Canadian fishes.

KEYS TO THE MONOGENEA AND TURBELLARIA

1 Body dorsoventrally flattened, posterior region modified to form attachment zone lacking sclerotized components at all stages of development .... Turbellaria (marine)

Body dorsoventrally flattened, posterior region modified to form distinct haptor (attachment organ) carrying sclerotized components (some of which may, rarely, be vestigial in adult worms) .... Monogenea (marine, brackish water, freshwater)

CLASS TURBELLARIA[1] (Ehrenberg, 1831)

Platyhelminthes: generally free-living, rarely symbiotic (commensalistic, ectoparasitic, endoparasitic, phoretic) with various aquatic organisms. Body surface usually partially or completely ciliated and containing rhabdites; attachment organs not uncommon but lacking sclerotized components. Generally hermaphroditic; life cycle usually lacking larval stage(s).

NEOOPHORA Westblad, 1948[2]

Turbellaria: ovary functionally divided into germarium (producing ova) and vitellarium (producing yolk); eggs ectolecithal; cleavage modified by presence of yolk.

ORDER SERIATA Westblad, 1935[3]

Neoophora: body elongate; statocyst present or not. Pharynx tubiform, plicate, directed posteriorly; intestine diverticulate. Testes and vitelline follicles in serially arranged, longitudinal rows.

Suborder TRICLADIDA Lang, 1884 (=EUSERIATA Westblad, 1952)[4]

Seriata: statocyst absent. Intestine with three diverticulate branches (one anterior, two posterior). One pair ovaries, copulatory bursa usually present; two or numerous testes, penis papilla present. Gonopore single.

PROCERODIDAE Diesing, 1862[5]

Tricladida: eye spots present or absent. Copulatory bursa rudimentary or well developed, variable in position. Testes two or numerous with vasa deferentia confluent or not; penis short or long. Usually free-living in littoral zone associated with areas near freshwater outfall, rarely symbiotic. One genus, *Micropharynx*, on Canadian fishes.

Micropharynx Jägerskiöld, 1896 (Fig. 1:0)

Procerodidae: body unpigmented, lacking eye spots and auricles; posterior region with well-defined adhesive zone. Pharynx small, in midbody region; anterior branch of intestine extending anterior to ovaries, posterior branches anastomosing or not. Testes numerous; vasa deferentia confluent behind pharynx; penis papilla conical, lying in well-developed, muscular atrium. Bursal canal with small vesicle (= copulatory bursa?); vitelline follicles numerous. On body surface of elasmobranchs. One species on Canadian fishes.

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[1] Dr Lesley Fleming, Department of Biology, University of New Brunswick, Fredericton, provided expert guidance on the diagnoses for many of the turbellarian taxa.

[2] Sensu Ax (1963). The rank of this taxon is debatable.

[3] Sensu Karling (1974).

[4] Sensu Hyman (1951).

[5] Based on de Beauchamp (1961).

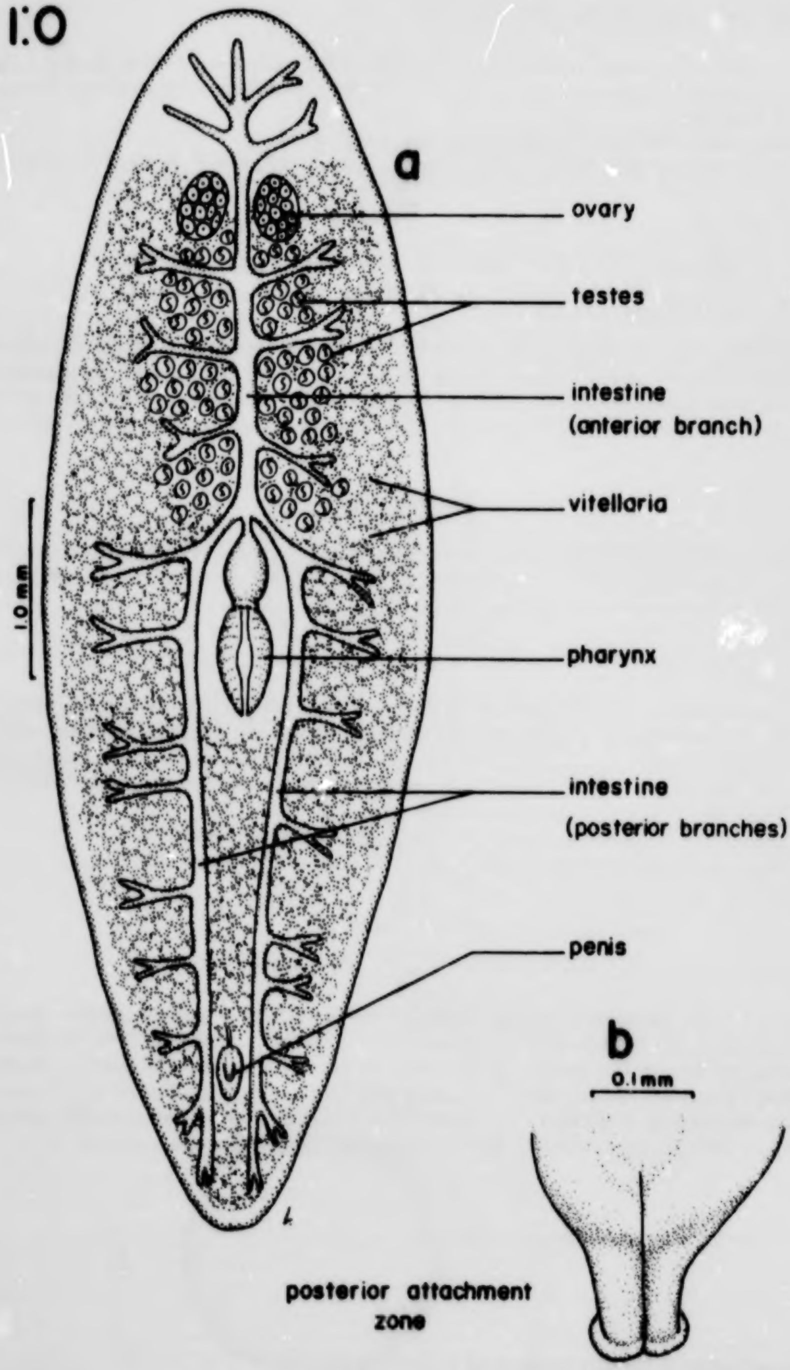
1:0
a
ovary
testes
intestine
(anterior branch)
vitellaria
1.0 mm
pharynx
intestine
(posterior branches)
penis
b
0.1 mm
posterior attachment
zone

FIG. 1:0. *Micropharynx* — generic characters (modified from Ball and Khan 1976): a. whole animal, ventral view; b. ventral view of infolded posterior region.

Micropharynx parasitica Jägerskiöld, 1896 (Fig. 1:0)

Descriptive and morphometric data (from Ball and Khan 1976): body ovate or oblong, up to 7 mm long by up to 4 mm wide; posterior end rounded or rolled inward with flat attachment zone. Anterior branch of intestine with preovarian diverticula.

On body surface of *Raja laevis* (1,2,3); *R. radiata* (4)
Records: 1. Stafford 1904 (Atl); 2. 1907 (Atl); 3. Cooper 1915 (Atl); 4. Ball and Khan 1976 (Atl)

ORDER UDONELLIDA[6] Ivanov and Mamkaev, 1973
(=UDONELLIDAE van Beneden and Hesse, 1863)

Neoophora: body elongate, cylindrical, with posterior, glandular, sucker-like adhesive organ lacking both highly developed musculature and sclerotized hooks (or hamuli). Head gland secretions granular and eosinophilic. Eye spots absent. Intestine simple, tubular, ending blindly. Testis single, in midbody region; ovary pretesticular; vitelline follicles relatively few, large. Larval stage lacking cilia. One genus, *Udonella*, on Canadian fishes.

Udonella Johnston, 1835 (Fig. 2:0)

Udonellida: anterior end of body bilobed with pair of glands. Genital pore ventral, submarginal on left side in pharyngeal region. Vagina (or copulatory bursa) absent. Egg with long filament with distal expansion. Adults attached to ectoparasitic copepods on marine fishes. One species on Canadian fishes.

Udonella caligorum Johnston, 1835 (Fig. 2:0)

Descriptive and morphometric data (from Price 1938a): body cylindrical, 1.1–1.4 mm long by 0.25 mm wide, anterior end with retractile area, 0.04–0.06 mm wide; posterior sucker 0.2 mm in diameter with two submarginal clusters of gland cells near posterior end of body proper. Pharynx, 0.15 by 0.09 mm, partly protrusible and anterior in position. Testis 0.08–0.10 mm in diameter; ovary 0.13 mm in diameter. Vitellaria a few large follicles. Eggs 133 by 42, with single filament at one pole.

On body surface of *Gadus morhua* (1,2);[7] *Hippoglossus hippoglossus* (3,4)[8]
Records: 1. Stafford 1904 (Atl); 2. 1907 (Atl); 3. Ronald 1958 (Atl); 4. 1960 (Atl)

CLASS MONOGENEA Carus, 1863

Platyhelminthes: generally permanent ectoparasites on body surface or gills of marine, brackishwater, or freshwater fishes (more rarely endoparasites in nasal cavities, ureters, urinary bladder, or alimentary canal of fishes, amphibians, reptiles, or mammals). Attachment by posterior adhesive organ (i.e. haptor) developed from larval haptor.[9] Hermaphroditic; life cycle direct with free-swimming, ciliated larva (oncomiracidium) with armed haptor bearing up to 16 marginal hooks. Adult haptor usually elaborated by addition of sclerotized hamuli and/or clamps, tegumentally derived squamodiscs or muscular suckers.

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[6] The taxonomic affiliations of *Udonella* are discussed in Appendix 3.
[7] Attached to an unidentified *Caligus* sp.
[8] Attached to *Lepeophtheirus hippoglossi*.
[9] Except in *Pseudacanthocotyla* see p. 17.

2:0

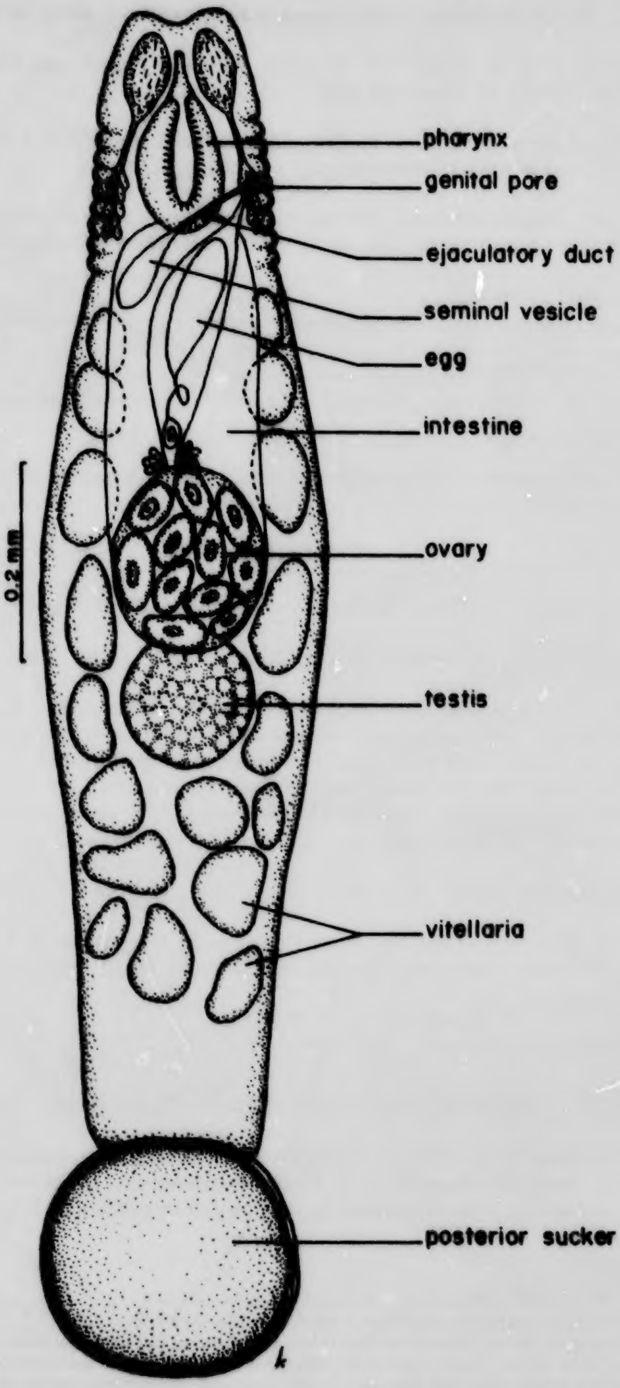
pharynx
genital pore
ejaculatory duct
seminal vesicle
egg
intestine
0.2 mm
ovary
testis
vitellaria
posterior sucker
k

FIG. 2:0. *Udonella* — generic characters (modified from Price 1938a): whole animal, ventral view.

Key to the major monogenean taxa parasitizing fishes of Canada

1 Haptor reduced to small sucker-like cleft (Fig. 3:0); marginal hooks vestigial, present only in larva. On body surface of elasmobranchs .... Microbothriidae (Family)[10]

Haptor distinct, formed from larval haptor; marginal hooks functional and persistent in adult. On elasmobranchs and teleosts (freshwater and marine) 2

2 Haptor complex, often subdivided, with paired muscular suckers (Fig. 38:0) or clamps (Fig. 43:0). Mouth surrounded by oral sucker (Fig. 40:0) or with paired suckers within buccal cavity (Fig. 42:0) .... Polyopisthocotylida (Order)

Haptor simple, entire, without paired suckers or clamps (Fig. 5:0). Mouth lacking oral sucker or buccal suckers 3

3 Haptor with 16 marginal hooks, one pair of hamuli. Viviparous, vitellaria absent or only weakly developed .... Gyrodactylida (Order)

Haptor with 14 or (rarely) 16 marginal hooks, none, one or two pairs of hamuli. Oviparous, vitellaria well developed .... Dactylogyrida (Order)

MICROBOTHRIIDAE Price, 1936[11]

One genus, *Microbothrium*, on Canadian fishes.

Microbothrium Olsson, 1869 (Fig. 3:0)

Body flattened with small, muscular, cup-shaped haptor lacking sclerotized components in adult; concavity of entire ventral body surface used in attachment. Anteriorly, two sucker-like structures opening into oral cavity; pharynx globular; intestinal caeca diverticulate, nonconfluent posteriorly. Testis simple follicular mass in midbody; penis sclerotized, tubular; genital pore median or submedian. Ovary anterior to testis, submedian; vagina opening close to genital pore, submedian. Vitellaria coextensive with gut caeca. Marine, on elasmobranchs. One species on Canadian fishes.

Microbothrium apiculatum Olsson, 1869 (Fig. 3:0)

Descriptive and morphometric data (from Price 1938a): body 1.7–3.2 mm by 0.70–1.6 mm; haptor oval, slit-like, opening 150-225 long, unarmed. Pharynx 190–300 long. Testis spherical, 340–510 diameter; seminal receptacle 40–115 diameter.

On body surface of *Squalus acanthias*
Records: Stafford 1904 (Atl); 1907 (Atl)

ORDER DACTYLOGYRIDA[12] Bykhovsky, 1937

Haptor entire.[13] Marginal hooks 14 or 16 in number (or secondarily reduced) with posterior-most pair (I) migrating anteriorly from peripheral to more central position; pair II between hamuli. Hamuli present or absent: if present, one or two pairs, supported by one, two or three transverse bars. Mouth lacking either oral sucker or buccal suckers. Oviparous.

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[10] The taxonomic affinities of the Microbothriidae are discussed in Appendix 3.

[11] An acceptable diagnosis for the Microbothriidae is not, in the author's opinion, currently available — see Appendix 3.

[12] Sensu Llewellyn (1970) for the "Dactylogyrideans", which Llewellyn regarded as a designation of convenience for a homogeneous group of parasites which is not identical with Bykhovsky's (1957) group bearing a similar name: in Llewellyn's scheme the tetraonchoideans (cited as tetraonchoidideans) were included and the monocotylids excluded.

[13] In the Acanthocotylidae the larval haptor persists without further development and is functionally replaced by a pseudohaptor.

3:0

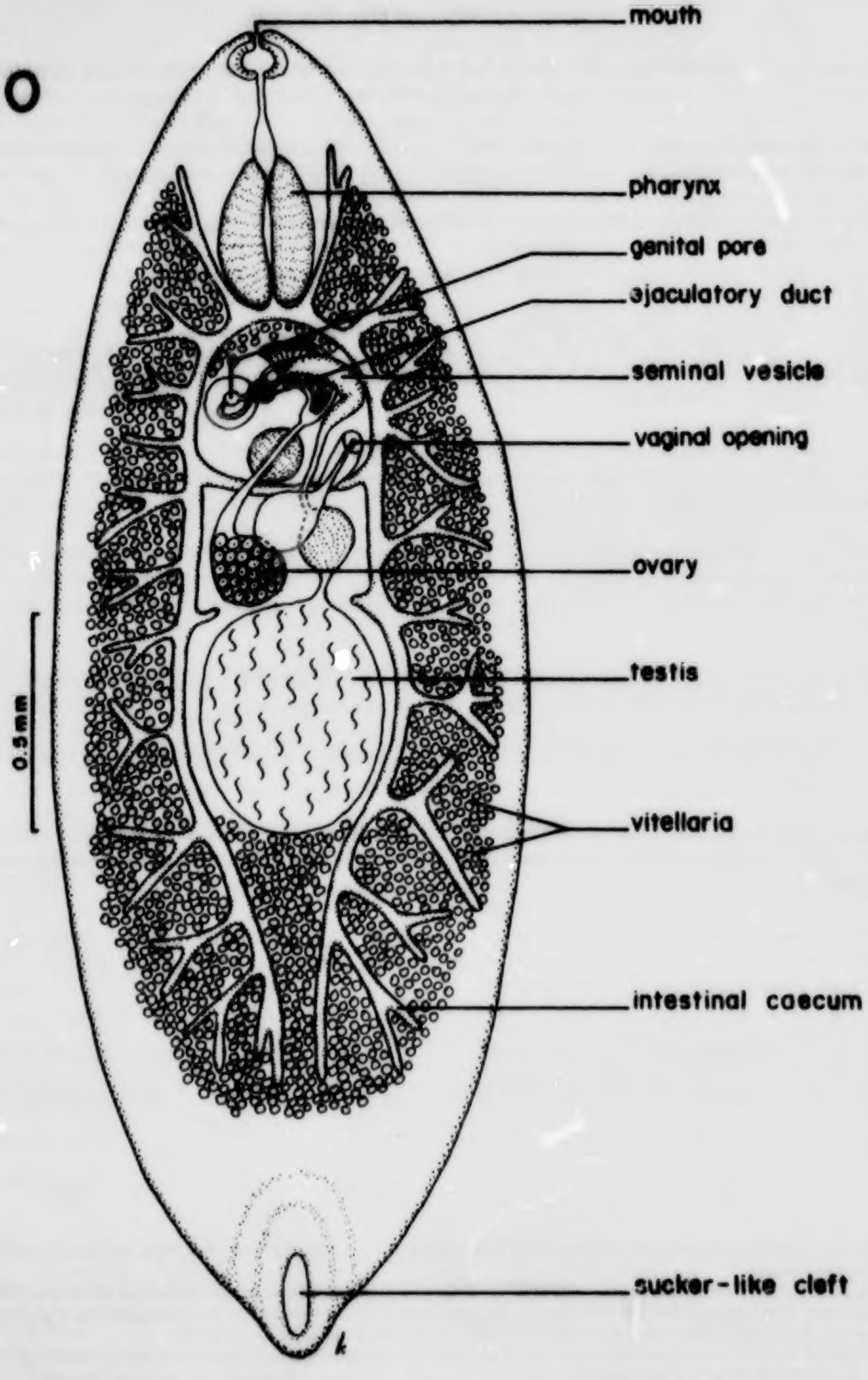
mouth
pharynx
genital pore
ejaculatory duct
seminal vesicle
vaginal opening
ovary
testis
vitellaria
intestinal caecum
sucker-like cleft
k
0.5mm

FIG. 3:0. *Microbothrium* — generic characters (modified from Dawes 1946): whole animal, ventral view.

Key to families of Dactylogyrida

1 Larval haptor persists but adult adhesive mechanism a secondarily developed pseudohaptor (Fig. 4:0). On elasmobranchs,[14] rarely marine teleosts .... Acanthocotylidae

Larval haptor develops into the adult adhesive mechanism. On marine or freshwater teleosts, rarely elasmobranchs 2

2 Body usually flat, large. Haptor septate (Fig. 20:0) or nonseptate (Fig. 19:0), with well-developed muscles, utilizing suction for attachment to *skin* of host; anterior body with pair of disc-like (Fig. 19:0) or sessile (Fig. 21:0) adhesive organs. On marine teleosts,[15] rarely elasmobranchs. .... Capsalidae

Body usually cylindrical, small. Haptor, lacking "suction disc" musculature, with hamuli (Fig. 5:0) of prime importance for attachment to *gills* of host;[16] anterior body with head organs (Fig. 5:0). Primarily on freshwater teleosts[17] 3

3 Haptor with 16 marginal hooks, pairs II to VIII peripheral and pair I central in position; two pairs of hamuli (one dorsal, one ventral) and single transverse bar (Fig. 32:0). On gills of salmonids and esocids .... Tetraonchidae

Haptor with 14 marginal hooks, pairs II to VII peripheral and pair I central in position; primarily one or two pairs of hamuli and one, two or three transverse bars.[18] Hamuli and bars may be secondarily reduced or lacking. Primarily on gills of freshwater teleosts, other than salmonids and esocids 4

4 Ovary looping right intestinal caecum (Fig. 29:0); penis U-shaped with complex accessory piece comprising two or three arms (Fig. 29:1b, 30:1b). On catostomids ..... Pseudomurraytrematidae

Ovary not looping right intestinal caecum; penis generally curved tube of varying size and shape but not forming U 5

5 Haptor with two pairs of hamuli (usually one pair dorsal and one ventral) each supported by transverse bar (usually one dorsal and one ventral) (Fig. 6:0). Typically (but not exclusively) on Perciformes .... Ancyrocephalidae

Haptor usually with one pair of hamuli (dorsal) which articulate with dorsal transverse bar;[19] reduced ventral bar and vestigial ventral hamuli[20] may or may not be present (Fig. 26:0). Typically (but not exclusively) on Cypriniformes .... Dactylogyridae

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[14] According to Yamaguti (1963) the only exception is *Lophocotyle cyclophora* Braun, 1896, recorded from the skin of *Notothenia* sp. from Brazilian waters.

[15] The genus *Entobdella* is an exception. Although most species occur on teleosts, a few parasitize elasmobranchs.

[16] Hamuli have been lost secondarily in some genera e.g. *Anonchohaptor, Icelanonchohaptor, Acolpenteron*, and *Pseudacolpenteron*.

[17] The genus *Salsuginus*, found on cyprinodontids inhabiting brackish water, is an exception.

[18] If one pair of hamuli, one or two bars are present; if two pairs, two or three bars are present (one ventral and two submedian dorsal).

[19] Hamuli and bar may be lost secondarily.

[20] Mizelle and Price (1963) described an additional pair of marginal hooks (designated as 4A) which Kearn (1968) considered to be vestigial hamuli.

ACANTHOCOTYLIDAE Price, 1936

Dactylogyrida: body almost rectangular with parallel sides. Anteriorly, two groups of glands open on petaloid head organs. Functional organ of attachment pseudohaptor with radiating rows of spines or muscular ridges; larval haptor undeveloped, attached to posterior region of pseudohaptor. Larval haptor with 16 marginal hooks: 14 peripheral and 2 central in position (Kearn 1967). Mouth ventral, caeca simple or branched, not confluent posteriorly. Testes numerous or few, postovarian, intercaecal; opening of copulatory complex median or submedian. Uterine pore marginal or submarginal. Vitellaria extending along length of caeca. Marine, typically (but not exclusively) on elasmobranchs. One genus, *Pseudacanthocotyla*, on Canadian fishes.

Pseudacanthocotyla Yamaguti, 1963 (Fig. 4:0)

Acanthocotylidae: functional pseudohaptor with numerous, radiating rows of spines. Pharynx globular, caeca simple. Testes numerous, seminal vesicle bipartite; prostatic vesicles paired, copulatory complex with muscular sac. Ovary entire, median or submedian; uterus opening on right side at, or behind, level of pharynx; seminal receptacle present. On elasmobranchs (rays).

Key to species of *Pseudacanthocotyla*

1 Number of rows of spines of pseudohaptor about 20; total number of spines about 150. Number of testes 32–37 .... *P. williamsi* Price, 1938 (Fig. 4:0, Table 1)
On gills of *Sebastes alutus*
Record: Sekerak and Arai 1973 (Pac)
Remarks: Sekerak and Arai (1973) considered this record of *P. williamsi*, which normally occurs on elasmobranchs, may be the result of interhost transfer in the trawl net during host capture.

Number of rows of spines on pseudohaptor about 30; total number of spines more than 300. Number of testes "about" 57 .... *P. verrilli* (Goto, 1899) Yamaguti, 1963 (Table 1)
On body surface of *Raja radiata*
Records: Stafford 1904 (Atl); 1907 (Atl); Threlfall 1969 (Atl); Gaevskaya and Umnova 1977 (Atl)

TABLE 1. Comparative measurements (in mm) of *Pseudacanthocotyla* spp. (Acanthocotylidae) recorded from fishes of Canada.

Species	*P. verilli*	*P. williamsi*
Source of data	Price (1938a)	Price (1938a)
Body: length	3.5–3.89	3.7–4.4
width	1.2–1.3	1.3–1.6
Pseudohaptor: width	1.28–1.36	1.2–1.3
Rows of spines: number	30	20 (rarely 21)
Larval haptor: width	0.13	0.06–0.07
Testes: number	about 57	32–37[a]
Eggs: length[b]	0.26	0.27
width	0.08	0.07
Site	skin	gills
Host	*Raja radiata*	*Sebastes alutus*
Locality	Atlantic	Pacific

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[a] Price (1938a) gives the number of testes as 32–57 and depicts 34 in his figure of *P. williamsi*. Sproston (1946) gives 32–37 in her key to species which is quoted herein.

[b] Excluding filament.

4:0

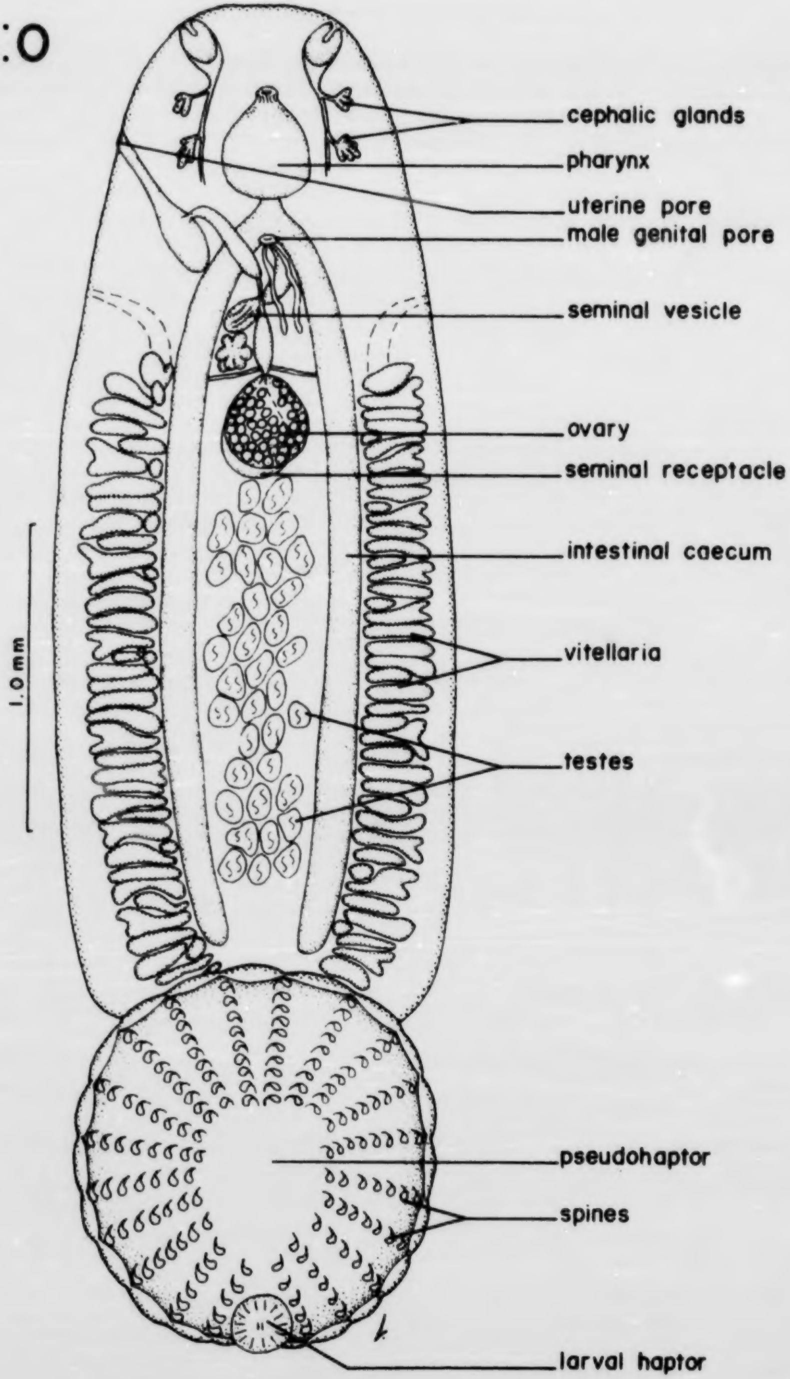
cephalic glands
pharynx
uterine pore
male genital pore
seminal vesicle
ovary
seminal receptacle
intestinal caecum
vitellaria
testes
1.0mm
pseudohaptor
spines
larval haptor

FIG. 4:0. *Pseudacanthocotyla* — generic characters (based on Price 1938a): whole animal, ventral view.

ANCYROCEPHALIDAE (Bykhovsky, 1937, subfam.) Bykhovsky and Nagibina, 1978

Dactylogyrida: body small, anterior extremity with cephalic lobes; head organs present; cephalic glands in two groups in anterolateral region of body. Two pairs of eyes. Haptor more or less distinct with 14 marginal hooks, 12 peripheral and two central in position; two pairs hamuli present (usually one pair dorsal and one ventral), each supported by transverse bar. Mouth ventral, pharynx present, muscular, intestinal caeca confluent. Testis intercaecal, postovarian; vas deferens looping dorsoventrally round left intestinal caecum, expanding to form seminal vesicle; penis sclerotized, tubular with variable accessory piece. Ovary pyriform or elongate, not looping round intestine; vaginal pore single, lateral, submarginal or median. Freshwater or brackish water, typically (but not exclusively) on Perciformes.

Key to genera of Ancyrocephalidae

1 Penis sclerotized, tubular, elongate, narrow, forming spiral with 4–6 turns and inflated base (Type 3, Fig. 9:1e).[21] In pharyngeal cavity (usually not on gills or associated structures) of centrarchids .... *Leptocleidus*

Penis sclerotized, tubular, comparatively short, never forming spiral. Typically on gills (rarely on body surface or in nasal cavities) of centrarchids, cyprinodontids, ictalurids, percids or percopsids ... 2

2 Penis straight or slightly curved with one or two spiral filaments (Type 2, Fig. 12:2g). On gills of Perciformes (centrarchids or percids) 3

Penis straight, bowed or curved, lacking spiral filaments 6

3 Distal tip of penis protruding through proximal aperture ("keyhole") of accessory piece (Fig. 12:4h). In life, haptor wedge-shaped (Fig. 12:0) with most marginal hooks oriented anteriorly; marginal hooks markedly different in shape (Fig. 12:4e, f, g) and size (pairs I and III–VII with long, inflated handle and short shaft). Typically on centrarchids .... *Onchocleidus*

Distal tip of penis protrudes through accessory piece or associated structures but "keyhole" not present. In life, haptor flat with most marginal hooks oriented radially (Fig. 6:0); marginal hooks almost equal in shape and size (pairs I and III-VII with short, uninflated handle and elongate shaft (Fig. 6:1e) 4

4 Distal tip of penis protruding through chelate accessory piece which has two well sclerotized, semicircular components one of which arises from posteriorly directed "handle" (Fig. 8:1f). Dorsal hamuli markedly larger than ventral hamuli (Fig. 8:0). On centrarchids .... *Haplocleidus*

Distal tip of penis protruding through sheath associated with filaments/accessory piece. Dorsal and ventral hamuli more or less equal in size 5

5 Penis with loosely spiraling filaments supporting voluminous sheath (Fig. 13:1f) into which accessory piece is incorporated. Hamuli with blunt, finger-like projection on inner curve of blade (Fig. 13:1a, c). Vagina on right side of body. On centrarchids .... *Pterocleidus*

Penis with spiraling filaments supporting sheath to which accessory piece is attached (Fig. 6:3f, g). Hamuli lacking finger-like projection. Vagina on left side of body.[22] On percids (Etheostomatini) .... *Aethycteron*

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[21] For explanation of "penis" types, see Appendix 4.

[22] See generic diagnosis for *Aethycteron*.

6 **Penis tubular, relatively short and robust, straight or curved; accessory piece single unit, with distal finger-like projection and bifid base (Type 1, Fig. 5:6f, g). On centrarchids** **7**

Penis tubular, relatively long and delicate, bowed or curved; accessory piece not as in Type 1 ..... **9**

7 Transverse bars of haptor articulating to form single supporting unit for hamuli, both pairs projecting ventrally (Fig. 5:0) .... *Actinocleidus*

Transverse bars of haptor not articulating; one pair hamuli projecting ventrally, one dorsally .. 8

8 Hamuli elongate, lacking superficial and deep roots, points projecting laterally beyond haptoral margin to give characteristic lyre-shaped appearance (Fig. 11:0) .... *Lyrodiscus*

Hamuli relatively short with obvious superficial and deep roots (Fig. 7:2a, c), points not projecting laterally beyond haptoral margin (Fig. 7:0) .... *Cleidodiscus*

9 Penis tubular, strongly bowed or curved. On cyprinodontids (*Fundulus* spp.) or ictalurids (*Ictalurus* spp., *Noturus* sp.) 10

Penis tubular, not bowed, slightly curved. On Perciformes (centrarchids or percids) or percopsids 11

10 Accessory piece with one or more distal hook-like structures and firm proximal attachment to base of penis (Type 4, Fig. 10:2f, g). Hamuli slender, strongly curved (Fig. 10:2a,c). Transverse bars with median lightly sclerotized flange (Fig. 10:2b, d). On ictalurids .... *Ligictaluridus*

Accessory piece lacking distal hook-like structures, not attached to base of penis (Type 5, Fig. 14:1f, g). Hamuli robust, strongly curved (Fig. 14:2a, c). Transverse bars lacking median flange (Fig. 14:1b, d). On cyprinodontids .... *Salsuginus*

11 Penis well sclerotized, with proximal handle-like region and distal, tubular ejaculatory region (Type 7, Fig. 16:1f); accessory piece with two distally fused rami, proximally one (Fig. 16:2g) or both (Fig. 16:1g) rami attached to penis at junction of handle/ejaculatory region. On percids or percopsids .... *Urocleidus*

Penis lightly sclerotized, tubular, lacking a proximal handle-like region (Type 6, Fig. 15:1f); accessory piece a single elongate, grooved structure, lying alongside penis. On centrarchids .... *Tetracleidus*

Actinocleidus Mueller, 1937 (Fig. 5:0)

Ancyrocephalidae: two pairs of hamuli both projecting ventrally; transverse bars articulating to form single supporting unit; marginal hooks of similar size and shape except that hooks of pair II have smaller handle. Copulatory complex (Type 1) comprising sclerotized, tubular penis with inflated base and heavily sclerotized accessory piece with distal finger-like projection and bifid base. Vagina sclerotized or not, opening on left side of body, leading to seminal receptacle. Vitellaria coextensive with intestine, extending laterally to body margin. On gills of North American freshwater fishes (Centrarchidae).

5:0

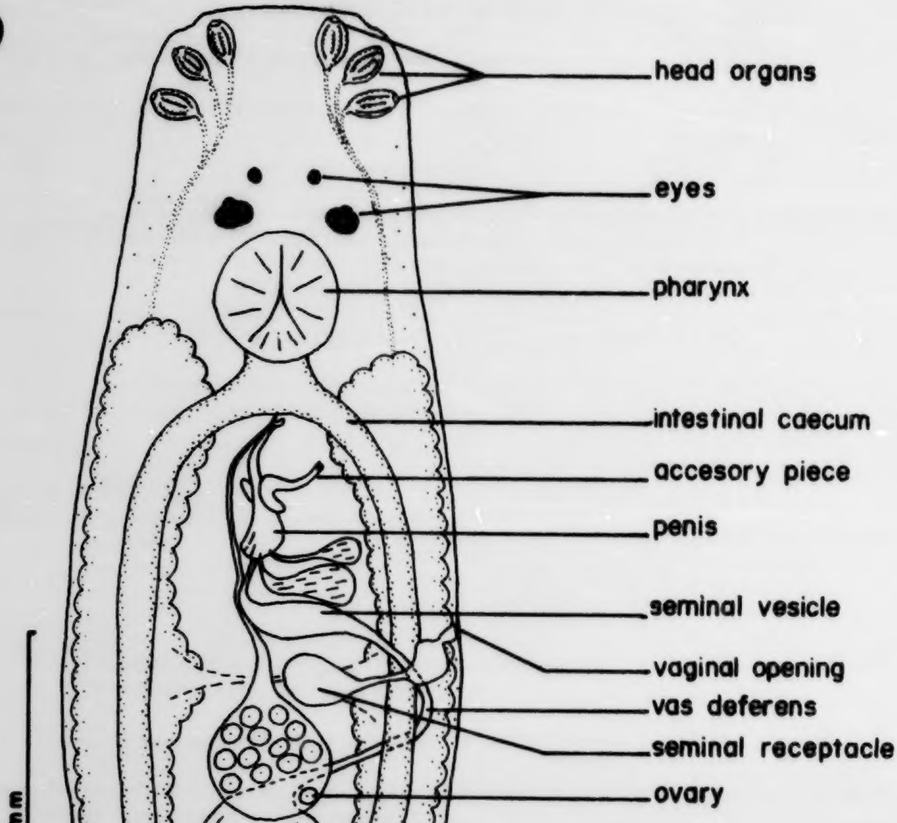
head organs
eyes
pharynx
intestinal caecum
accesory piece
penis
seminal vesicle
vaginal opening
vas deferens
seminal receptacle
ovary
testis
vitellaria
marginal hook
hamuli
transverse bars
0.2 mm

FIG. 5:0. *Actinocleidus* — generic characters (original): whole animal, ventral view.

Key to species of *Actinocleidus*

1 Posterior bar plate-like, almost rectangular; hamuli with distinct deep root 2

Posterior bar not plate-like but with two lateral, posteriorly directed extensions; hamuli usually[23] with reduced deep root 3

2 Hamuli more than 40 long, bars comparatively large; penis less than 45 long .... *A. fusiformis* (Mueller, 1934) Mueller, 1937 (Fig. 5:2, Table 2)
Syn: *Syncleithrium fusiformis* (Mueller, 1934) Price, 1967
On gills of *Micropterus dolomieui* (1,2,3,6); *M. salmoides* (2,4,5)
Records: 1. Cooper 1915 (Ont); 2. Dechtiar 1972b (Ont); 3. 1972c (Ont); 4. Hanek and Fernando 1972b (Ont); 5. Molnar et al. 1974 (Ont); 6. Lubinsky and Loch 1979 (Man)

Hamuli less than 30 long; bars comparatively small; penis more than 49 long .... *A. mizellei* Hanek and Fernando, 1972 (Fig. 5:5, Table 2)
On gills of *Micropterus salmoides*
Record: Hanek and Fernando 1972a (Ont)

3 Penis more than 35 long 4

Penis less than 35 long 5

4 Posterior bar with posterior extensions laterally inflated; hamuli with reduced deep root .... *A. oculatus* (Mueller, 1934) Mueller, 1937 (Fig. 5:6, Table 2)
On gills of *Lepomis gibbosus*
Records: Mizelle and Donahue 1944 (Ont); Dechtiar 1972b (Ont); Beverley-Burton 1981 (Ont)

Posterior bar with posterior extensions not laterally inflated; hamuli with distinct deep root .... *A. unguis* Mizelle and Cronin, 1943 (Fig. 5:8, Table 2)
On gills of *Lepomis macrochirus*
Record: Dechtiar 1972b (Ont)

5 Posterior bar with posterior extensions laterally inflated 6

Posterior bar with posterior extensions not laterally inflated .... *A. bakeri* Mizelle and Cronin, 1943 (Fig. 5:1, Table 2)
On gills of *Lepomis macrochirus*
Record: Dechtiar 1972b (Ont)

6 Vagina heavily sclerotized, conspicuous ...... *A. recurvatus* Mizelle and Donahue, 1944 (Fig. 5:7, Table 2)
On gills of *Lepomis gibbosus*
Records: Mizelle and Donahue 1944 (Ont); Dechtiar 1972b (Ont); Hanek and Fernando 1972a (Ont); 1975 (Ont); 1978a (Ont); 1978d (Ont); Cone 1980 (NB); Beverley-Burton 1981 (Ont)

Vagina only lightly sclerotized or nonsclerotized, inconspicuous 7

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[23] Except in *A. unguis*.

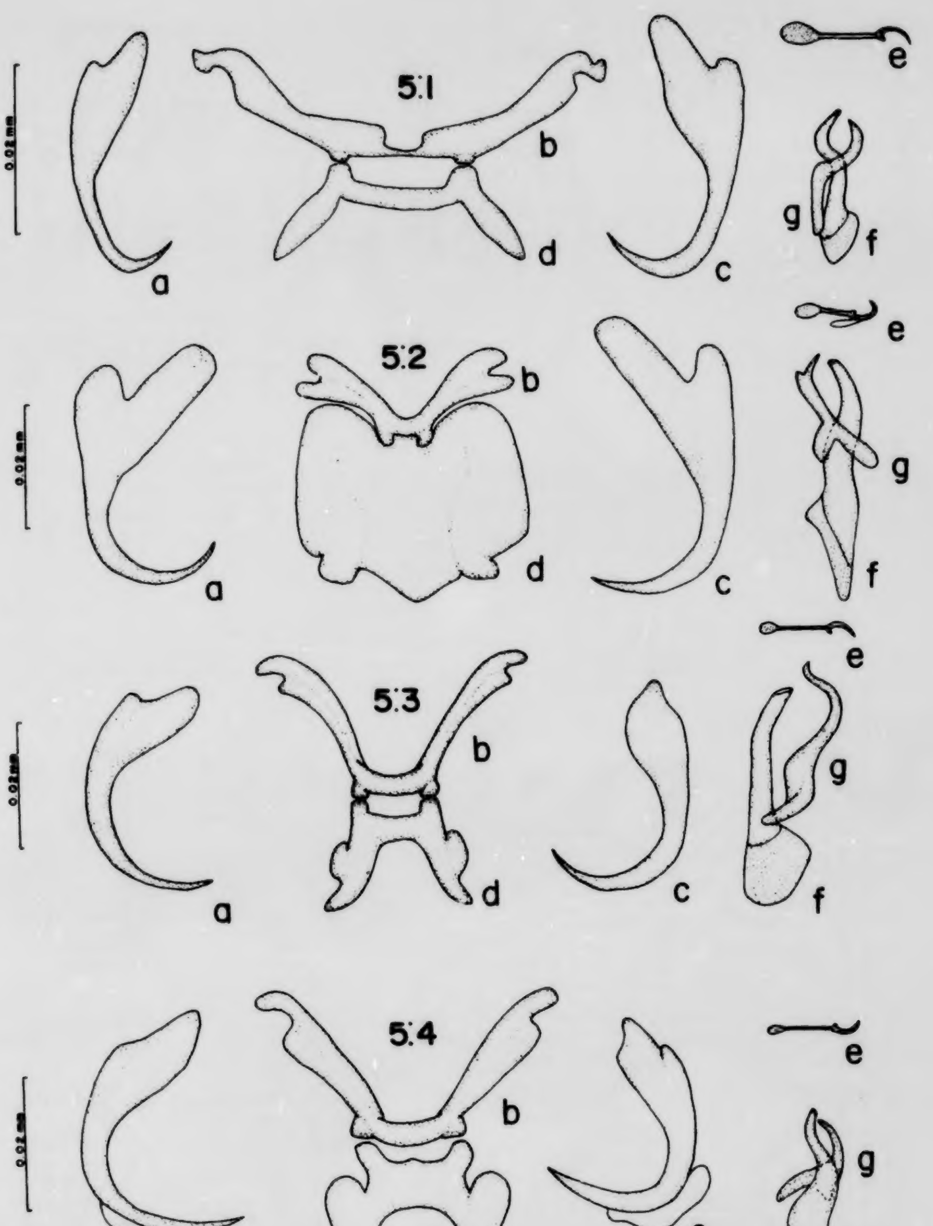

FIG. 5:1–5:4. *Actinocleidus* spp. 5:1. *A. bakeri* (modified from Mizelle and Cronin 1943): a. anterior hamulus; b. anterior bar; c. posterior hamulus; d. posterior bar; e. marginal hook; f. penis; g. accessory piece. 5:2. *A. fusiformis* (a–d modified from Mueller 1936a, e–g from Price 1967a): a. anterior hamulus; b. anterior bar; c. posterior hamulus; d. posterior bar; e. marginal hook; f. penis; g. accessory piece. 5:3. *A. gibbosus* (modified from Mizelle and Donahue 1944): a. anterior hamulus; b. anterior bar; c. posterior hamulus; d. posterior bar; e. marginal hook; f. penis; g. accessory piece. 5:4. *A. incus* (modified from Mizelle and Donahue 1944): a. anterior hamulus; b. anterior bar; c. posterior hamulus; d. posterior bar; e. marginal hook; f. penis; g. accessory piece.

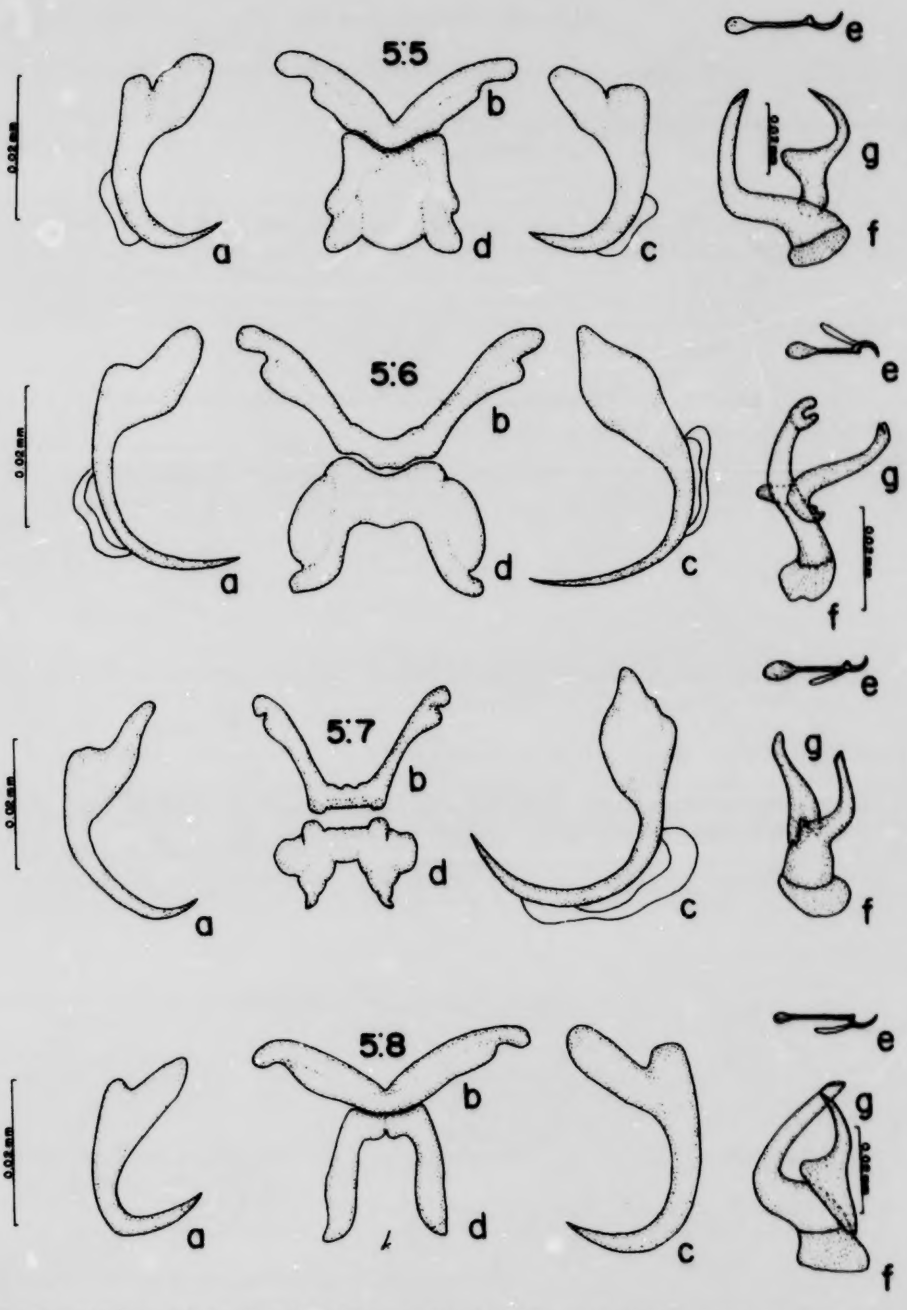

FIG. 5:5–5:8. *Actinocleidus* spp. 5:5. *A. mizellei* (modified from Hanek and Fernando 1972a): a. anterior hamulus; b. anterior bar; c. posterior hamulus; d. posterior bar; e. marginal hook; f. penis; g. accessory piece. 5:6. *A. oculatus* (redrawn from Beverley-Burton 1981): a. anterior hamulus; b. anterior bar; c. posterior hamulus; d. posterior bar; e. marginal hook; f. penis; g. accessory piece. 5:7. *A. recurvatus* (redrawn from Beverley-Burton 1981): a. anterior hamulus; b. anterior bar; c. posterior hamulus; d. posterior bar; e. marginal hook; f. penis; g. accessory piece. 5:8. *A. unguis* (modified from Mizelle and Cronin 1943): a. anterior hamulus; b. anterior bar; c. posterior hamulus; d. posterior bar; e. marginal hook; f. penis; g. accessory piece.

TABLE 2. Comparative measurements (in μm) of the species of *Actinocleidus* Mueller, 1937, recorded from fishes of Canada.

Species	*A. bakeri*	*A. fusiformis*	*A. gibbosus*	*A. incus*[a]	*A mizellei*	*A. oculatus*	*A. recurvatus*	*A. unguis*
Source of data	Mizelle and Cronin (1943)	Hanek and Fernando (1972a)	Hanek and Fernando (1972a)	Mizelle and Donahue (1944)	Hanek and Fernando (1972a)	Beverley-Burton (1981)	Beverley-Burton (1981)	Mizelle and Cronin (1943)
Body: length	555 (536–571)	1224–1692	372–528	281 (198–342)	1495 (1104–1616)[b]	220 (168–267)	175 (150–230)	999–1256[c]
width	69 (64–71)	146–168	58–82	52 (43–120)	264 (204–276)	74 (49–97)	45 (40–60)	221–321
Anterior hamuli: length	29 (27–31)	43–45	26–28	33 (27–39)	27 (24–28)	34 (28–40)	38 (32–40)	26–32
Anterior bar: transverse length	46 (43–51)	69–72	36–39	41 (31–54)	32 (29–34)	44 (38–47)	42 (40–45)	32
median width	—	9–10	4–5	—	4 (4–5)	4 (4–5)	7 (5–10)	—
Posterior hamuli: length	30 (29–32)	49–52	25–27	35 (30–41)	26 (26–28)	35 (25–39)	34 (32–40)	32
Posterior bar: transverse length	31 (28–32)	38–42	16–18	30 (21–34)	17 (14–18)	28 (22–33)	28 (25–33)	18
median width	—	42–44	12–14	—	14 (13–17)	6 (5–7)	7 (5–8)	—
Marginal hooks: length	14–19	16–21	12–14	12–17	14–19	14 (12–17)	18 (15–20)	14–20
Penis: length	23 (21–26)	37–41	20–22	24 (18–34)	58 (50–64)	40 (38–46)	23 (20–30)	44–46
Accessory piece: length	17 (16–18)	24–26	19–21	17 (13–22)	32 (27–34)	28 (20–29)	12 (10–15)	35
Site	gills	gills	gills	gills	gills	gills	gills	gills
Host(s)	*Lepomis macrochirus*	*Micropterus salmoides*	*Lepomis gibbosus* *Lepomis macrochirus*	*Lepomis gibbosus*	*Micropterus salmoides*	*Lepomis gibbosus*	*Lepomis gibbosus*	*Lepomis macrochirus*
Locality(ies)	Ontario	Manitoba Ontario	Ontario	Ontario	Ontario	Ontario	New Brunswick Ontario	Ontario

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[a] *A. scapularis* and *A. sigmoideus* are considered synonyms of *A. incus* which was described from one specimen. Thus, measurements quoted are those originally designated for *A. sigmoideus*.

[b] Holotype and, in parentheses, paratypes.

[c] Two specimens.

7 **Posterior bar 16–18 transverse length ...... *A. gibbosus* Mizelle and Donahue, 1944 (Fig. 5:3, Table 2)**
On gills of *Lepomis gibbosus* (1,3,4,5); *L. macrochirus* (2)
Records: 1. Mizelle and Donahue 1944 (Ont); 2. Hanek and Fernando 1972a (Ont); 3. 1975 (Ont); 4. 1978a (Ont); 5. 1978d (Ont)

Posterior bar 21–34 transverse length ... *A. incus* Mizelle and Donahue, 1944 (Fig. 5:4, Table 2)
Syn: *A. scapularis* Mizelle and Donahue, 1944 (new syn.)
A. sigmoideus Mizelle and Donahue, 1944 (new syn.)
On gills of *Lepomis gibbosus*
Record: Mizelle and Donahue 1944 (Ont)
Remarks: Mizelle and Donahue (1944) proposed five species of *Actinocleidus* from *L. gibbosus* taken in Algonquin Park, Ontario (*A. gibbosus, A. incus, A. recurvatus, A. scapularis* and *A. sigmoideus*). Additional data have been provided for *A. gibbosus* and *A. recurvatus* (see Hanek and Fernando (1972a) and Beverley-Burton (1981), respectively), which are considered valid. However, a comparison of *A. incus, A. scapularis,* and *A. sigmoideus* indicated there were no real distinguishing features. Mizelle and Donahue (1944) claimed a difference in shape of the male copulatory complex of *A. scapularis* but they figured an end-on view of an uncompressed specimen. Because *A. incus* has page priority, *A. scapularis* and *A. sigmoideus* are declared synonyms of *A. incus*. The morphometric data provided by Mizelle and Donahue (1944) for *A. incus* and *A. scapularis* (which were described from single specimens) lie within the ranges for *A. sigmoideus* which are therefore quoted in Table 2.

Aethycteron Suriano and Beverley-Burton, 1982 (Fig. 6:0)

Ancyrocephalidae: two pairs of hamuli (one dorsal, one ventral); transverse bars not articulating with each other; marginal hooks of similar shape and size. Copulatory complex (Type 2) comprising sclerotized, tubular, penis with inflated base and two spiral filaments supporting more or less voluminous sheath; accessory piece lightly sclerotized, variable in shape, attached to penis sheath. Vagina inconspicuous in some species,[24] nonsclerotized, opening on left side of body, leading to seminal receptacle. Vitellaria coextensive with intestine, extending laterally to body margin. On gills of North American freshwater fishes (Percidae: Etheostomatini).

Key to species of *Aethycteron*

1 Penis not more than 40 long; vagina inconspicuous 2

Penis more than 45 long; vagina well defined 4

2 Transverse bars comparatively robust, dorsal bar 36–48 transverse length, ventral bar 33–49 transverse length; penis 31-40 long ....
.... **A. malleus** (Mueller, 1938) Suriano and Beverley-Burton, 1982 (Fig. 6:3, Table 3)
Syn: *Urocleidus malleus* (Mueller, 1938) Mizelle and Hughes, 1938
On gills of *Percina caprodes* (1,2,4); *Percina maculata* (3)
Records: 1. Dechtiar 1972b (Ont), 2. 1972c (Ont); 3. Suriano and Beverley-Burton 1982 (Ont); 4. Lubinsky and Loch 1979 (Man)

Transverse bars not more than 30 transverse length; penis 23–30 long 3

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[24] Gusev (1978) stated that a vaginal opening, vagina and seminal receptacle are, apparently, present in all dactylogyridans and because a nonsclerotized vagina is difficult to observe, the descriptive term "vagina absent" is not acceptable. While studying living specimens of *A. hargisi, A. malleus,* and *A. micropercae*, motile sperm were seen in the seminal receptacle to the left of the oviduct but a vaginal pore and duct were not observed. Hence the use of "vagina inconspicuous".

6:0

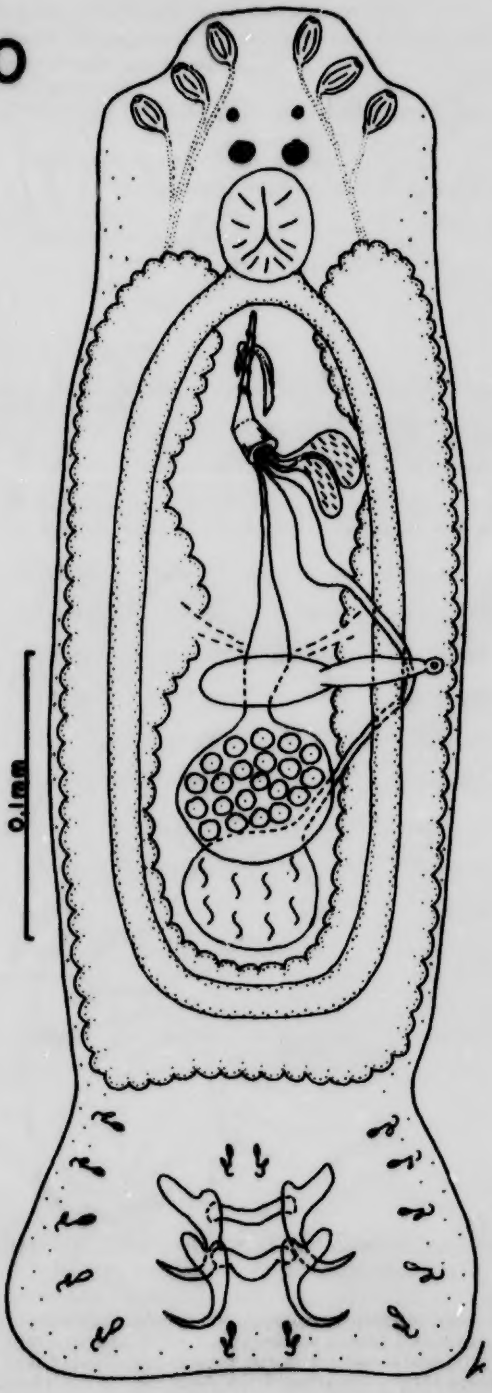

FIG. 6:0. *Aethycteron* — generic characters (original): whole animal, ventral view.

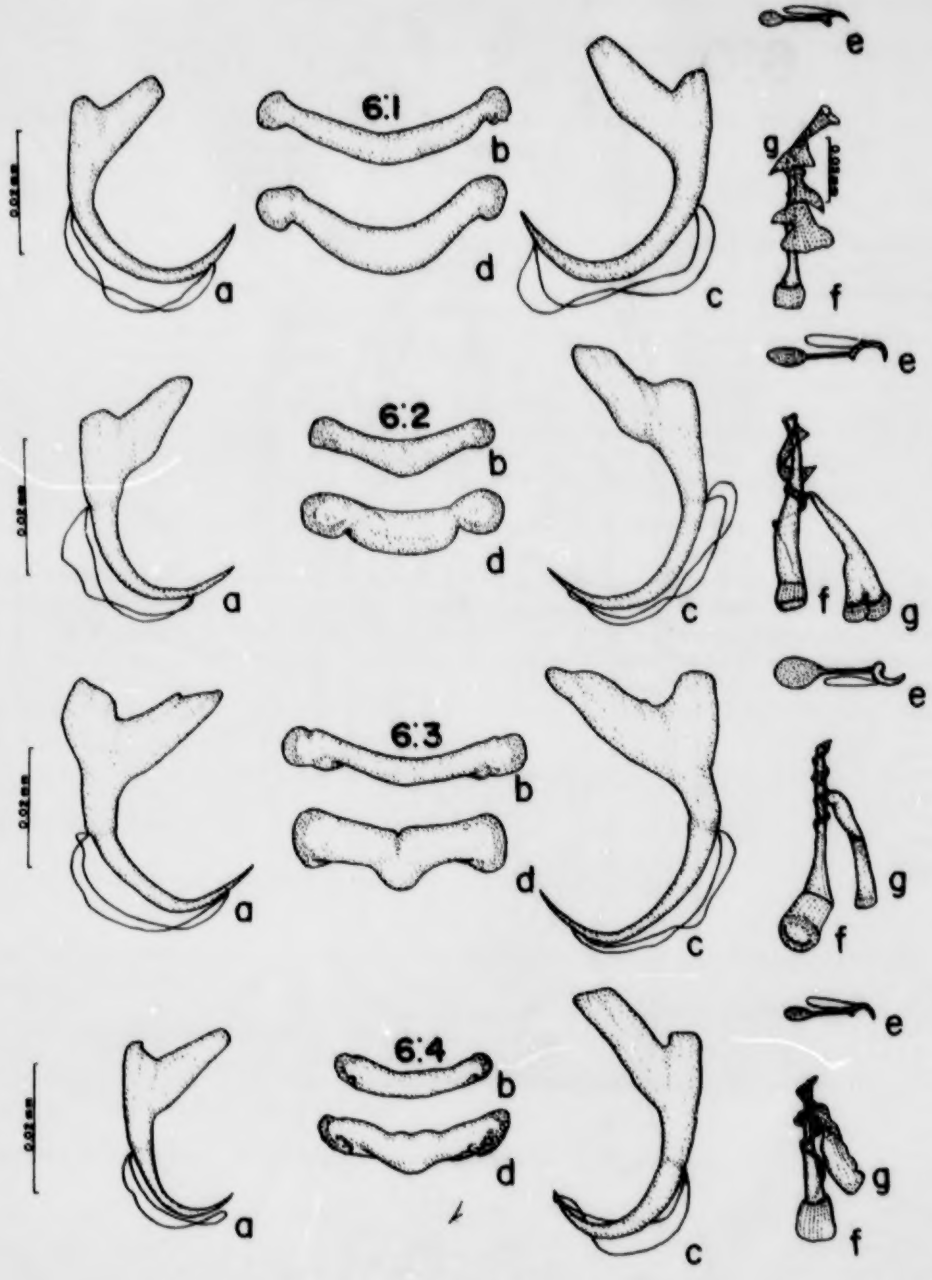

FIG. 6:1–6:4. *Aethycteron* spp. 6:1. *A. caerulei* (redrawn from Suriano and Beverley-Burton 1982): a. dorsal hamulus; b. dorsal bar; c. ventral hamulus; d. ventral bar; e. marginal hook; f. penis; g. accessory piece. 6:2. *A. hargisi* (redrawn from Suriano and Beverley-Burton 1982): a. dorsal hamulus; b. dorsal bar; c. ventral hamulus; d. ventral bar; e. marginal hook; f. penis; g. accessory piece. 6:3. *A. malleus* (redrawn from Suriano and Beverley-Burton 1982): a. dorsal hamulus; b. dorsal bar; c. ventral hamulus; d. ventral bar; e. marginal hook; f. penis; g. accessory piece. 6:4. *A. micropercae* (redrawn from Suriano and Beverley-Burton 1982): a. dorsal hamulus; b. dorsal bar; c. ventral hamulus; d. ventral bar; e. marginal hook; f. penis; g. accessory piece.

3 Accessory piece with heavily sclerotized, bifid distal extremity ....
... *A. hargisi* (Hanek and Fernando, 1972) Suriano and Beverley-Burton, 1982 (Fig. 6:2, Table 3)
Syn: *Urocleidus hargisi* Hanek and Fernando, 1972
On gills of *Etheostoma nigrum*
Records: Hanek and Fernando 1972a (Ont); Suriano and Beverley-Burton 1982 (Ont)

Accessory piece lightly sclerotized, irregular in outline ....
.... *A. micropercae* Suriano and Beverley-Burton, 1982 (Fig. 6:4, Table 3)
On gills of *Etheostoma microperca*
Record: Suriano and Beverley-Burton 1982 (Ont)

TABLE 3. Comparative measurements (in μm)of the species of *Aethycteron* Suriano and Beverley-Burton, 1982, recorded from fishes of Canada (from Suriano and Beverley-Burton 1982).

Species	*A. caerulei*	*A. hargisi*	*A. malleus*	*A. micropercae*	*A. moorei*	*A. nigrei*
Body: length	406 (330–594)	509 (422–651)	490 (410–630)	456 (402–346)	424 (306–648)	450 (250–498)
width	138 (106–197)	184 (118–206)	206 (148–226)	128 (98–146)	133 (97–148)	175 (149–224)
Dorsal hamuli: length	35 (29–38)	31 (30–32)	36 (32–40)	28 (25–35)	43 (40–45)	36 (32–40)
Dorsal bar: transverse length	38 (34–40)	27 (26–30)	41 (36–48)	25 (22–30)	46 (45–50)	36 (34–40)
Ventral hamuli: length	36 (30–41)	35 (32–38)	38 (35–45)	34 (32–40)	47 (40–48)	39 (34–43)
Ventral bar: transverse length	36 (33–39)	27 (26–30)	41 (33–49)	28 (26–30)	47 (45–52)	41 (38–46)
Marginal hooks: total length	16 (15–17)	18 (15–20)[a]	18 (15–20)	13 (10–15)	15 (14–17)	16 (15–18)
Penis: length	65 (62–70)	26 (23–30)	33 (31–40)	25 (24–27)	62 (55–70)	50 (45–58)
Accessory piece: length	—	18 (14–20)	22 (18–27)	16 (15–18)	21 (18–24)	18 (15–19)
Vagina	left side	not seen	not seen	not seen	left side	left side
Site	gills	gills	gills	gills	gills	gills
Host(s)	*Etheostoma caeruleum*	*Etheostoma nigrum*	*Percina maculata* *P. caprodes*	*Etheostoma microperca*	*Etheostoma flabellare*	*Etheostoma nigrum*
Locality(ies)	Ontario	Ontario	Manitoba Ontario	Ontario	Ontario	Ontario

[a] Corrected data.

4 Hamuli and transverse bars well developed: dorsal hamuli 40–45 long, ventral hamuli 40–48 long; dorsal bar 45–50 transverse length, ventral bar 45–52 transverse length. Penis with distinct distal curvature and discrete accessory piece ....
.... *A. moorei* (Mizelle, 1940) Suriano and Beverley-Burton, 1982 (Fig. 6:5, Table 3)
On gills of *Etheostoma flabellare*
Record: Suriano and Beverley-Burton, 1982 (Ont)

Hamuli and transverse bars generally less developed 5

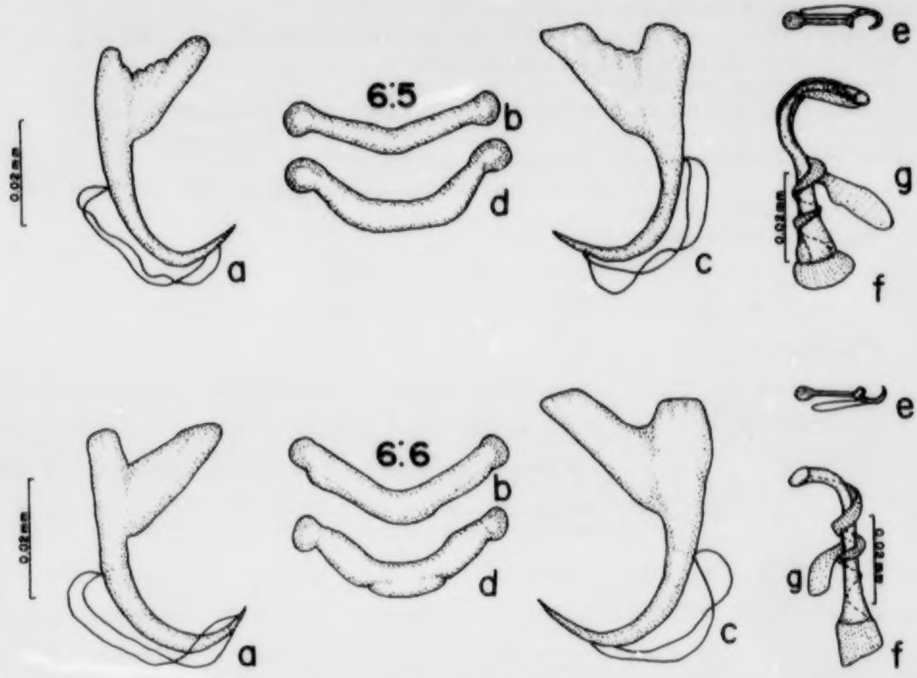

FIG. 6:5-6:6. *Aethycteron* spp. 6:5. *A. moorei* (redrawn from Suriano and Beverley-Burton 1982): a. dorsal hamulus; b. dorsal bar; c. ventral hamulus; d. ventral bar; e. marginal hook; f. penis; g. accessory piece. 6:6. *A. nigrei* (redrawn from Suriano and Beverley-Burton 1982): a. dorsal hamulus; b. dorsal bar; c. ventral hamulus; d. ventral bar; e. marginal hook; f. penis; g. accessory piece.

5 Dorsal hamuli 29-38 long, ventral hamuli 30-41 long; dorsal bar 34-40 transverse length, ventral bar 33-39 transverse length. Penis 62-70 long with slightly flared sheath and discrete accessory piece .... *A. caerulei* Suriano and Beverley-Burton, 1982 (Fig. 6:1, Table 3)

On gills of *Etheostoma caeruleum*
Record: Suriano and Beverley-Burton 1982 (Ont)

Dorsal hamuli 32-40 long, ventral hamuli 34-43 long, dorsal bar 34-40 transverse length, ventral bar 38-46 transverse length. Penis 45-58 long with slightly flared sheath and discrete accessory piece .... *A. nigrei* Suriano and Beverley-Burton, 1982 (Fig. 6:6, Table 3)

On gills of *Etheostoma nigrum*
Record: Suriano and Beverley-Burton 1982 (Ont)

Cleidodiscus Mueller, 1934 (Fig. 7:0)

Ancyrocephalidae: two pairs of hamuli (one dorsal, one ventral); transverse bars not articulating with each other; marginal hooks of similar shape and size. Copulatory complex (Type 1) comprising sclerotized tubular penis with inflated base and well-sclerotized accessory piece with distal, finger-like projection and bifid base. Vagina sclerotized or not, opening on left side of body, leading to seminal receptacle. Vitellaria coextensive with intestine, extending laterally to body margin. On gills of North American freshwater fishes (Centrarchidae and Cyprinidae).

7:0

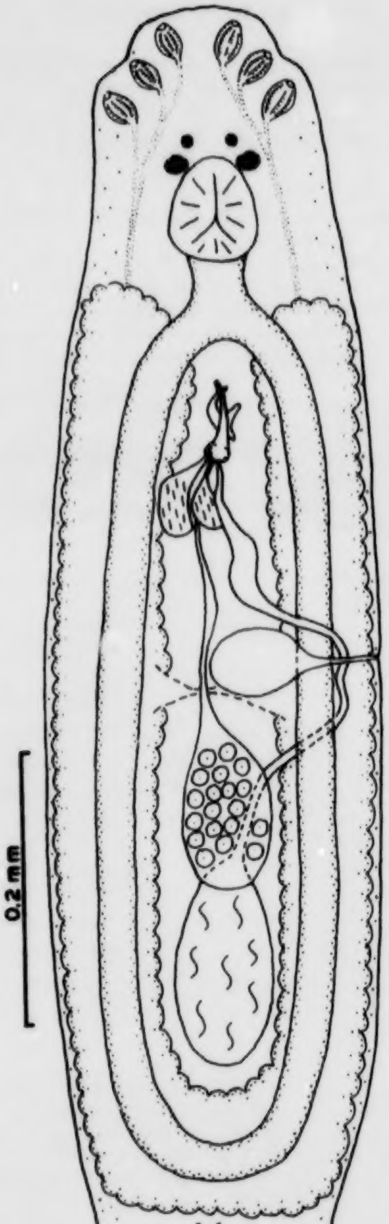

FIG. 7:0. *Cleidodiscus* — generic characters (original): whole animal, ventral view.

Key to species of *Cleidodiscus*

1 Adult body large and robust, 992–1600 long, compared with most other ancyrocephalids from North American freshwater fishes. On gills of centrarchids 2

Body of more typical ancyrocephalid size, 468–756 long. On gills of various cyprinids .... *C. brachus* Mueller, 1938 (Fig. 7:1, Table 4)

Syn: *Urocleidus brachus* (Mueller, 1938) Price, 1967

On gills of *Chrosomus eos* (6); *C. neogaeus* (2,5); *Couesius plumbeus* (4); *Platygobio gracilis* (3); *Semotilus atromaculatus* (1,6); *S. margarita* (6)

Records: 1. Dechtiar 1972b (Ont); 2. 1972c (Ont); 3. Arai and Chien 1973 (Alta); 4. Threlfall 1974 (Lab); 5. Lubinsky and Loch 1979 (Man); 6. Cone 1980 (NB)

Remarks: Beverley-Burton and Suriano (1980a) provided a revised diagnosis for *Cleidodiscus*. From a study of specimens of *C. brachus* (loaned by Dr D. Cloutman in August 1984) the generic affinity of this species is considered problematic. Although the penis/accessory piece complex may prove to be of the same type (1) as *C. robustus*, the morphology of the haptoral sclerites is dissimilar and none of the recorded hosts are centrarchids.

2 Penis 90–95; vagina with proximal spines .... *C. robustus* Mueller, 1934 (Fig. 7:2, Table 4)

On gills of *Lepomis gibbosus* (1,2,3,4,5); *L. macrochirus* (1)

Records: 1. Hanek and Fernando 1972a (Ont); 2. 1975 (Ont); 3. 1978a (Ont); 4. 1978d (Ont); 5. Beverley-Burton and Suriano 1980a (Ont)

Penis 39–64; vagina lacking proximal spines ...... *C. venardi* Mizelle and Jaskoski, 1942 (Fig. 7:3, Table 4)

On gills of *Lepomis macrochirus*

Record: Dechtiar 1972b (Ont)

TABLE 4. Comparative measurements (in μm) of the species of *Cleidodiscus* Mueller, 1934, recorded from fishes of Canada.

Species	*C. brachus*	*C. robustus*	*C. venardi*
Source of data	*Mizelle and* Klucka (1953)	Beverley-Burton and Suriano (1980a)	Mizelle and Jaskoski (1942)
Body: length	554 (468–756)	1360 (1100–1600)	992 (902–1043)
width	180 (144–198)	450 (400–500)	188 (169–226)
Dorsal hamuli: length	45 (43–46)	27 (25–28)	23 (22–24)
Dorsal bar: transverse length	29	33 (30–35)	25 (23–28)
Ventral hamuli: length	47 (45–48)	29 (28–30)	25 (22–27)
Ventral bar: transverse length	39 (36–42)	34 (32–35)	24 (23–27)
Marginal hooks: length	16–22	18 (15–20)	13–19
Penis: length	28 (27–29)	92 (90–95)	56 (39–64)
Accessory piece: length	22	55 (51–59)	42 (39–44)
Site	gills	gills	gills
Host(s)	*Chrosomus eos* *C. neogaeus* *Platygobio gracilis* *Semotilus atromaculatus* *S. margarita*	*Lepomis gibbosus* *L. macrochirus*	*Lepomis macrochirus*
Locality(ies)	Alberta Labrador Manitoba New Brunswick Ontario	Ontario	Ontario

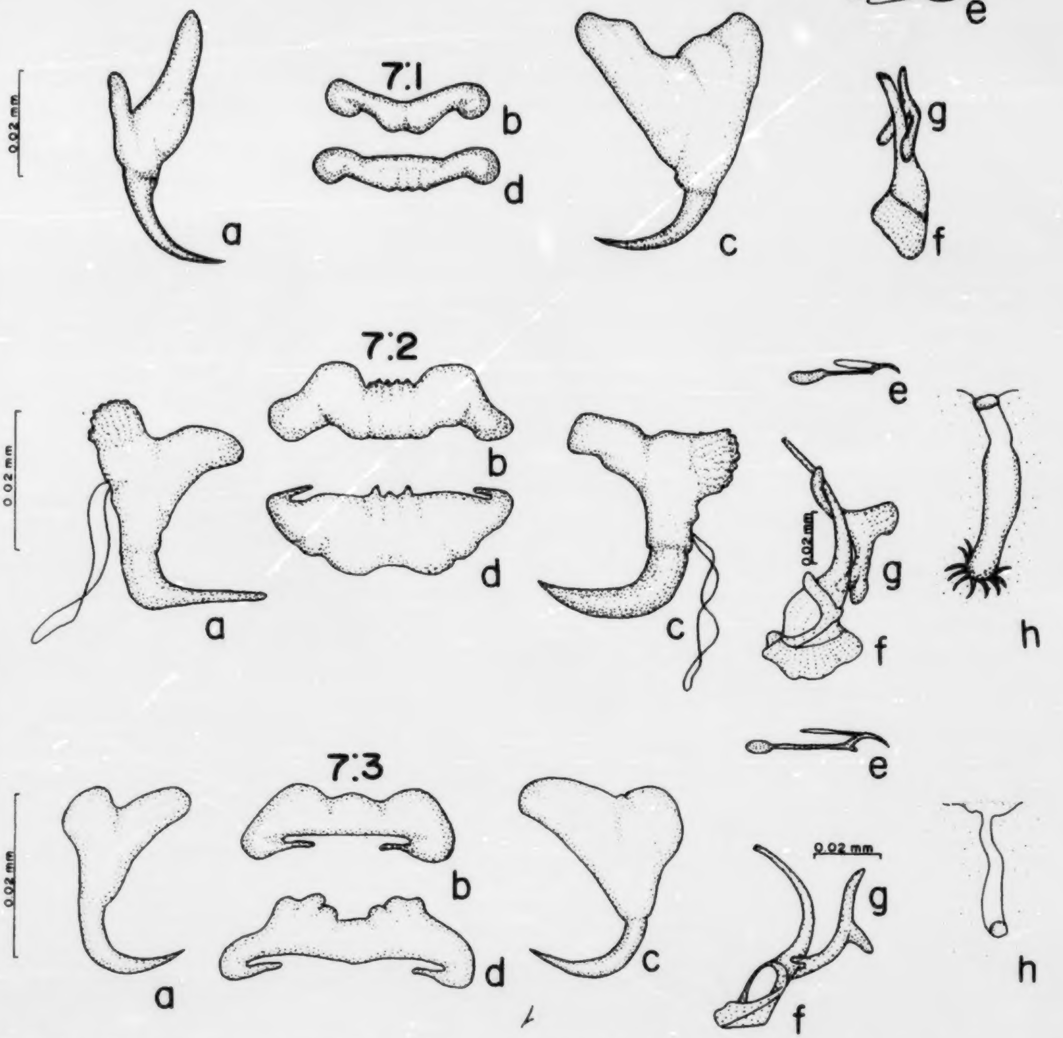

FIG. 7:1–7:3. *Cleidodiscus* spp. 7:1. *C. brachus* (b,d,e–g modified from Mueller 1938, a and c from Threlfall 1974): a. dorsal hamulus; b. dorsal bar; c. ventral hamulus; d. ventral bar; e. marginal hook; f. penis; g. accessory piece. 7:2. *C. robustus* (redrawn from Beverley-Burton and Suriano 1980a): a. dorsal hamulus; b. dorsal bar; c. ventral hamulus; d. ventral bar; e. marginal hook; f. penis; g. accessory piece; h. vagina. 7:3 *C. venardi* (modified from Mizelle and Jaskowski 1942): a. dorsal hamulus; b. dorsal bar; c. ventral hamulus; d. ventral bar; e. marginal hook; f. penis; g. accessory piece; h. vagina.

Records of unidentified *Cleidodiscus* spp.[25] are listed from:

Ambloplites rupestris, Lepomis macrochirus, Micropterus dolomieui — Dechtiar 1972b, Ontario; *Morone americana* — Tedla and Fernando 1969b, Ontario; *Perca flavescens, Percopsis omiscomaycus* — Dechtiar 1972b, Ontario; *Stizostedion vitreum vitreum* — Anthony 1976, Ontario.

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[25] *Cleidodiscus* sp. of Mizelle and Donahue (1944) from *Perca flavescens* was designated as *Urocleidus adspectus* Mueller, 1936 by Dechtiar (1974a). It is probable that most of the above records are misidentifications, at the generic level, of *Cleidodiscus* sensu Beverley-Burton and Suriano (1980a).

8:0

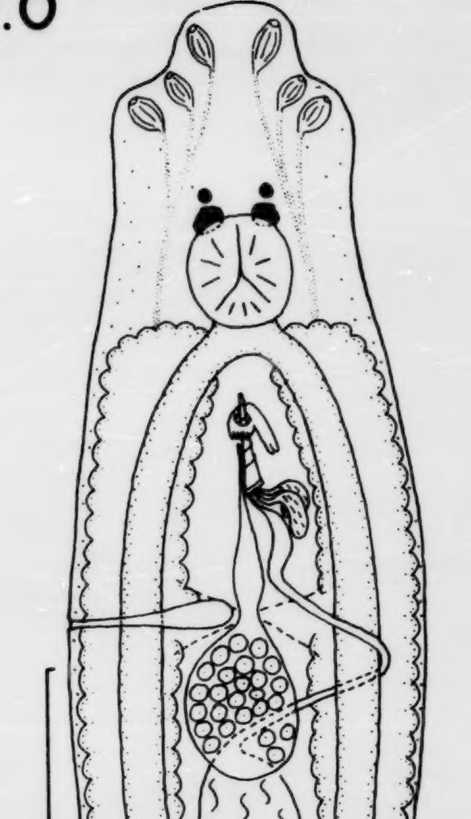

FIG. 8:0. *Haplocleidus* — generic characters (original): whole animal, ventral view.

Haplocleidus Mueller, 1937 (Fig. 8:0)

Ancyrocephalidae: two pairs of hamuli (one dorsal, one ventral) dorsal hamuli markedly larger than ventral; transverse bars not articulating with each other; marginal hooks of similar shape and size. Copulatory complex (Type 2) comprising sclerotized tubular penis with inflated base and two spiral filaments; accessory piece chelate with two sclerotized components (elongate shaft fused to distal, semicircular piece and second semicircular piece forming ring through which penis protrudes). Vagina nonsclerotized, opening on right side of body, leading to seminal receptacle. Vitellaria coextensive with intestine extending laterally to body margin. On gills of North American freshwater fishes (Centrarchidae).

Key to species of *Haplocleidus*

1 Dorsal hamuli 60–85 long, ventral hamuli 35–45 long ....
.... *H. dispar* (Mueller, 1936) Mueller, 1937 (Fig. 8:1, Table 5)

Syn: *Urocleidus dispar* (Mueller, 1936) Mizelle and Hughes, 1938

On gills of *Lepomis gibbosus* (1,3,5,6,7,8,9,10); *L. macrochirus* (2); *Micropterus dolomieui* (2,7); *M. salmoides* (4)

Records: 1. Mizelle and Donahue 1944 (Ont); 2. Hanek and Fernando 1972a (Ont); 3. 1975 (Ont); 4. Molnar et al. 1974 (Ont); 5. Cone and Anderson 1977 (Ont); 6. Hanek and Fernando 1978a (Ont); 7. 1978d (Ont); 8. Beverley-Burton and Suriano 1980b (Ont); 9. 1980c (Ont); 10. Cone 1980 (NB)

Remarks: Beverley-Burton and Suriano (1980b) recognized *Haplocleidus* and redescribed *H. dispar.*

Dorsal hamuli 45–47 long, ventral hamuli 21–23 long ....
.... *H. furcatus* Mueller, 1937 (Fig. 8:2, Table 5)

Syn: *Urocleidus furcatus* (Mueller, 1937) Mizelle and Hughes, 1938

On gills of *Micropterus salmoides*

Record: Hanek and Fernando 1972a (Ont)

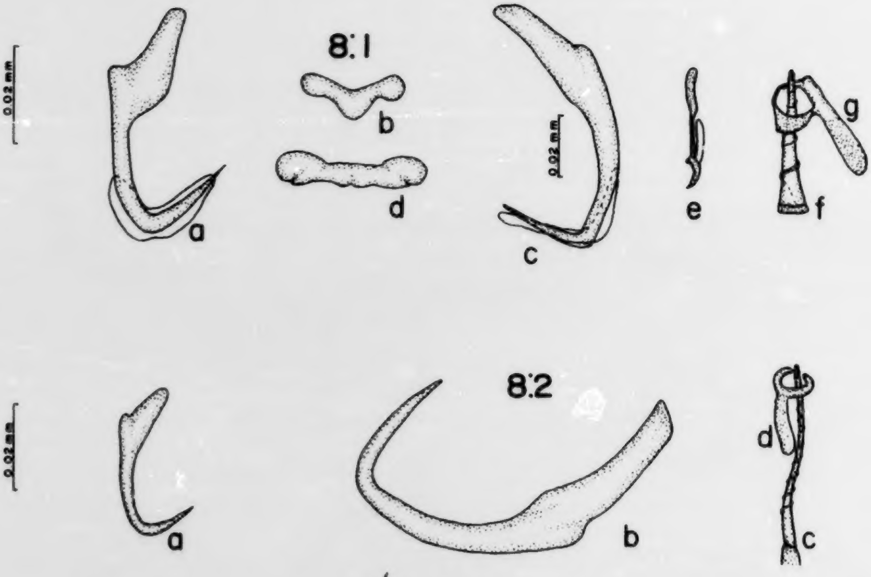

FIG. 8:1–8:2. *Haplocleidus* spp. 8:1. *H. dispar* (redrawn from Beverley-Burton and Suriano 1980b): a. dorsal hamulus; b. dorsal bar; c. ventral hamulus; d. ventral bar; e. marginal hook; f. penis; g. accessory piece. 8:2. *H. furcatus* (modified from Mueller 1937): a. dorsal hamulus; b. ventral hamulus; c. penis; d. accessory piece.

9:0

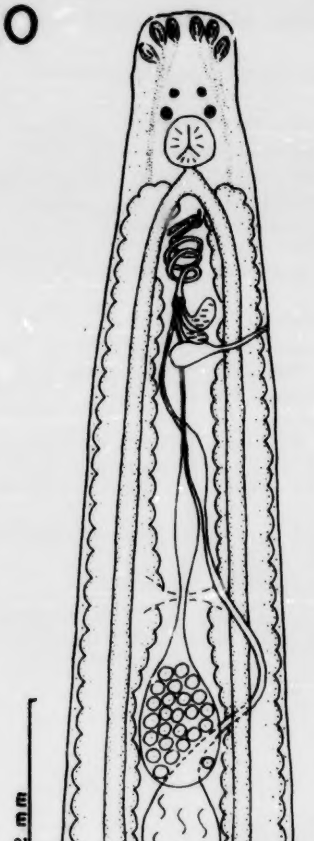

FIG. 9:0. *Leptocleidus* — generic characters (modified from Sullivan et al. 1978): whole animal, ventral view.

Leptocleidus Mueller, 1936 (Fig. 9:0)

Ancyrocephalidae: cephalic lobes poorly developed. Haptor not clearly set off from body, tapering posteriorly, with fimbriated lateral margins; two pairs of hamuli (one dorsal, one ventral); ventral bar present, dorsal bar lacking; marginal hooks of similar shape and size. Copulatory complex (Type 5) comprising sclerotized, elongate spiral penis with 4–6 turns and inflated base; accessory piece with distal guiding ring and proximal finger-like process. Vagina sclerotized, coiled and tubular, opening on left side of body, leading to seminal receptacle. Vitellaria coextensive with intestine, extending laterally to body margin. In pharyngeal area (usually not on gills or associated structures) of North American freshwater fishes (Centrarchidae). One species on Canadian fishes.

Leptocleidus megalonchus Mueller, 1936 (Fig. 9:1)

Morphometric data in Table 5.

Syn: *Urocleidus megalonchus* (Mueller, 1938) Price, 1967

On gills (?) of *Ambloplites rupestris* (1); *Lepomis gibbosus* (1); *Micropterus dolomieui* (2)

Records: 1. Stafford 1905[26] (unspecified locality); 2. Cooper 1915[27] (Ont)

Remarks: Sullivan et al. (1978) resurrected *Leptocleidus*, redescribed *L. megalonchus*, and specified that the species occurs in the pharyngeal area exclusive of the gills and associated structures. In both Canadian reports the presence of *L. megalonchus* on the gills is noted but this is, possibly, an error.

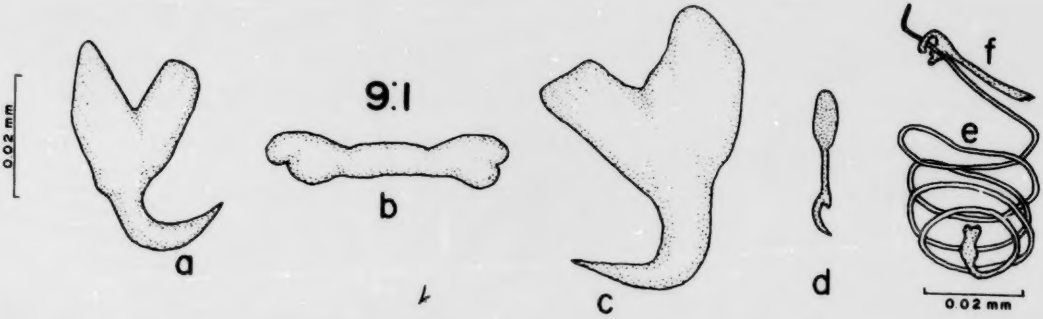

FIG. 9:1. *Leptocleidus megalonchus* (modified from Sullivan et al. 1978): a. dorsal hamulus; b. ventral bar; c. ventral hamulus; d. marginal hook; e. penis; f. accessory piece.

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[26] As *Tetraonchus unguiculatus* — see Margolis and Arthur (1979).

[27] As *Ancyrocephalus paradoxus* — see Margolis and Arthur (1979).

Ligictaluridus n. g.[28] (Fig. 10:0)

Ancyrocephalidae: two pairs of hamuli (one dorsal, one ventral); transverse bars not articulating with each other, with median, lightly sclerotized, flange; marginal hooks slightly dissimilar in shape and size. Copulatory complex (Type 4) comprising sclerotized, curving tubular penis with inflated base; accessory piece closely attached to penis base with well-sclerotized, blunt, proximal projection and elongate limb, bearing hook-like projection(s) distally. Vagina sclerotized or not, opening on left side of body, leading to seminal receptacle. Vitellaria coextensive with intestine, extending laterally to body margin and filling all available intercaecal space. On gills of North American freshwater fishes (Ictaluridae).

TABLE 5. Comparative measurements (in µm) of the species of *Haplocleidus* Mueller, 1937, *Leptocleidus* Mueller, 1936, and *Ligictaluridus* n. g., recorded from fishes of Canada.

Species	*H. dispar*	*H. furcatus*	*Leptocleidus megalonchus*	*Ligictaluridus floridanus*	*Ligictaluridus pricei*
Source of data	Beverley-Burton and Suriano (1980b)	Hanek and Fernando (1972a)	Sullivan et al. (1978)	material of Mueller (1936b)[d]	Klassen and Beverley-Burton (1985)
Body: length	410 (320–512)	540–696	568–1459	439 (307–600)	510 (280–810)
width	100 (90–150)	82–98	160–295	115 (73–147)	158 (70–405)
Dorsal hamuli: length	71 (60–85)	45–47	29–45	43 (39–50)	46 (39–53)
Dorsal bar: transverse length	30 (28–35)	23–25	lacking	76 (61–89)	51 (43–56)
Ventral hamuli: length	40 (35–45)	21–23	39–49	48 (41–56)	49 (45–61)
Ventral bar: transverse length	21 (17–25)	17–19	20–39	70 (64–81)	47 (40–52)
Marginal hooks: length	16 (15–20)[a]	14–19	21–29	14–17	13–17
Penis: length	31 (26–35)	26–31	52–105[b]	48 (42–55)	42 (40–48)
Accessory piece: length	20 (17–25)	19–22	50–62	43 (40–47)	28 (23–26)
Site(s)	gills	gills	gills, pharyngeal area[c]	gills	gills
Host(s)	*Lepomis gibbosus* *L. macrochirus* *Micropterus dolomieui* *M. salmoides*	*Micropterus salmoides*	*Ambloplites rupestris* *Lepomis gibbosus* *Micropterus dolomieui*	*Ictalurus punctatus*	*Ictalurus nebulosus*
Locality(ies)	New Brunswick Ontario	Ontario	Ontario	Ontario	Manitoba New Brunswick Ontario

[a] Pairs I–VII.
[b] With 4–6 loops.
[c] See remarks on *L. megalonchus* on p. 37.
[d] Measurements from Klassen and Beverley-Burton (1985).

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[28] See Klassen and Beverley-Burton (1985).

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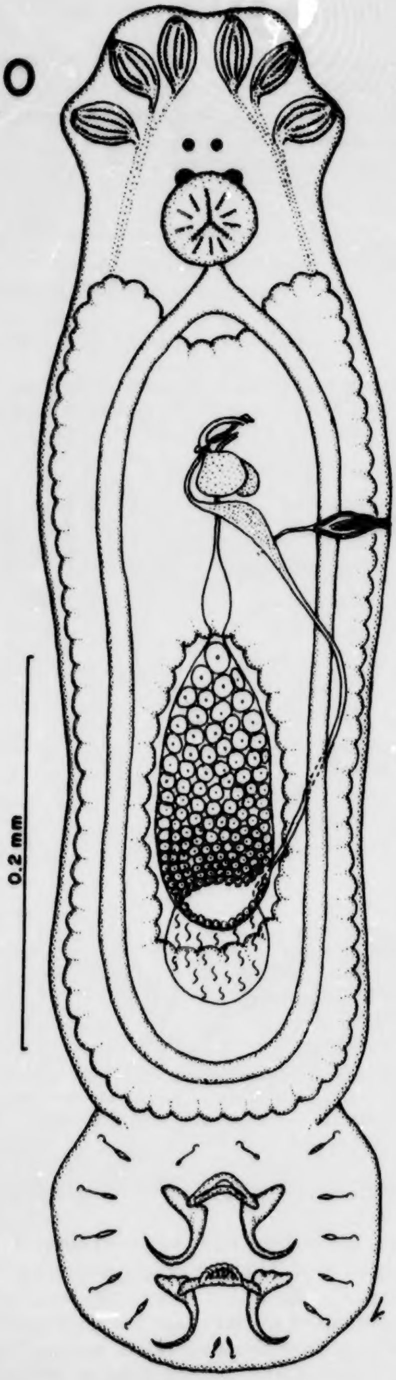

FIG. 10:0. *Ligictaluridus* — generic characters (original): whole animal, ventral view.

Key to species of *Ligictaluridus*

1 Dorsal transverse bar 61–89 transverse length, ventral bar 64–81; penis with distal, lightly sclerotized inflation; accessory piece with bifid distal extremity; vagina with distinctive cone-shaped structure matching penile funnel .... *L. floridanus* (Mueller, 1936) n. comb. (Fig. 10:1, Table 5)

Syn: *Cleidodiscus floridanus* Mueller, 1936
On gills of *Ictalurus nebulosus; I. punctatus; Noturus gyrinus*
Record: Dechtiar 1972b (Ont)

Dorsal transverse bar 43–56 transverse length, ventral bar 40–52; penis not inflated distally; accessory piece with undivided distal extremity; vagina inconspicuous .... *L. pricei* (Mueller, 1936) n. comb. (Fig. 10:2, Table 5)

Syn: *Cleidodiscus pricei* Mueller, 1936
On gills of *Ictalurus melas* (1); *I. nebulosus* (1,2,3,4,5,6,7,8); *I. punctatus* (2); *Noturus flavus* (2); *N. gyrinus* (2)
Records: 1. Mizelle and Donahue 1944 (Ont); 2. Dechtiar 1972b (Ont); 3. 1972c (Ont); 4. Hanek and Fernando 1972a (Ont); 5. Molnar et al. 1974 (Ont); 6. Lubinsky and Loch 1979 (Man); 7. Cone 1980 (NB); 8. Klassen and Beverley-Burton 1985 (Ont)

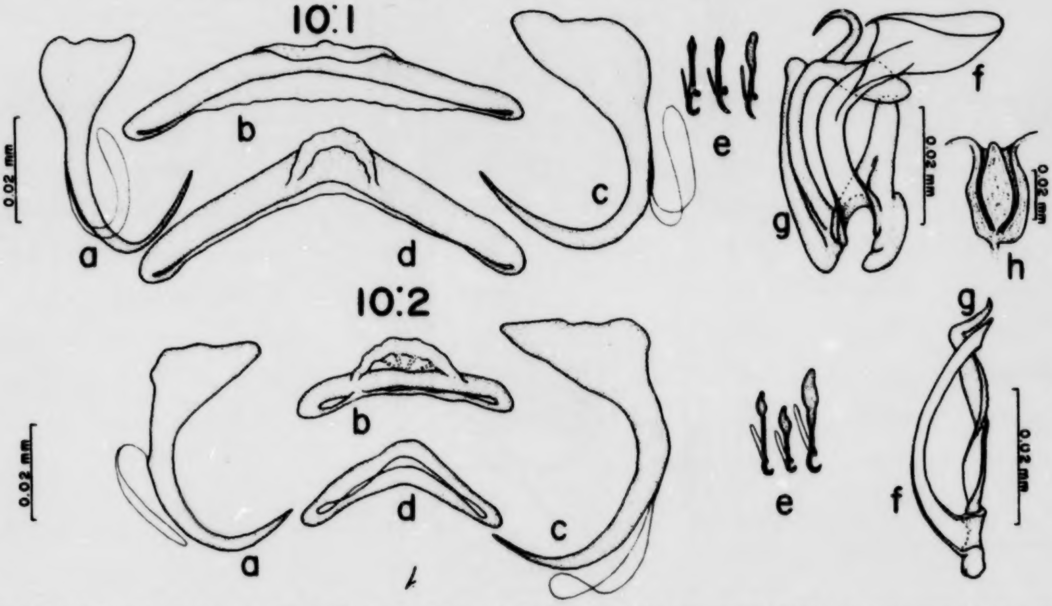

FIG. 10:1–10:2. *Ligictaluridus* spp. 10:1. *L. floridanus* (redrawn from Klassen and Beverley-Burton 1985): a. dorsal hamulus; b. dorsal bar; c. ventral hamulus; d. ventral bar; e. marginal hooks (I, II and III–VII); f. penis; g. accessory piece; h. vagina. 10:2. *L. pricei* (redrawn from Klassen and Beverley-Burton 1985): a. dorsal hamulus; b. dorsal bar; c. ventral hamulus; d. ventral bar; e. marginal hooks (I,II and III–VII); f. penis; g. accessory piece.

Lyrodiscus Rogers, 1967 (Fig. 11:0)

Ancyrocephalidae: haptor conspicuous, set off from body by stout peduncle. Two pairs of hamuli (one dorsal, one ventral), lacking deep and superficial roots but with points projecting from lateral margins of haptor to give characteristic inverted "lyre-shaped" appearance; transverse bars not articulating with each other, markedly different in shape; marginal hooks of similar shape but slightly different size. Copulatory complex (Type 1) comprising sclerotized, tubular penis with inflated base; accessory piece well sclerotized with distal, finger-like projection and bifid base. Vagina sclerotized, opening on left side of body, lateral or submedian. Vitellaria coextensive with intestine. On fins and body surface (rarely in nasal cavities) of North American freshwater fishes (Centrarchidae).

11:0

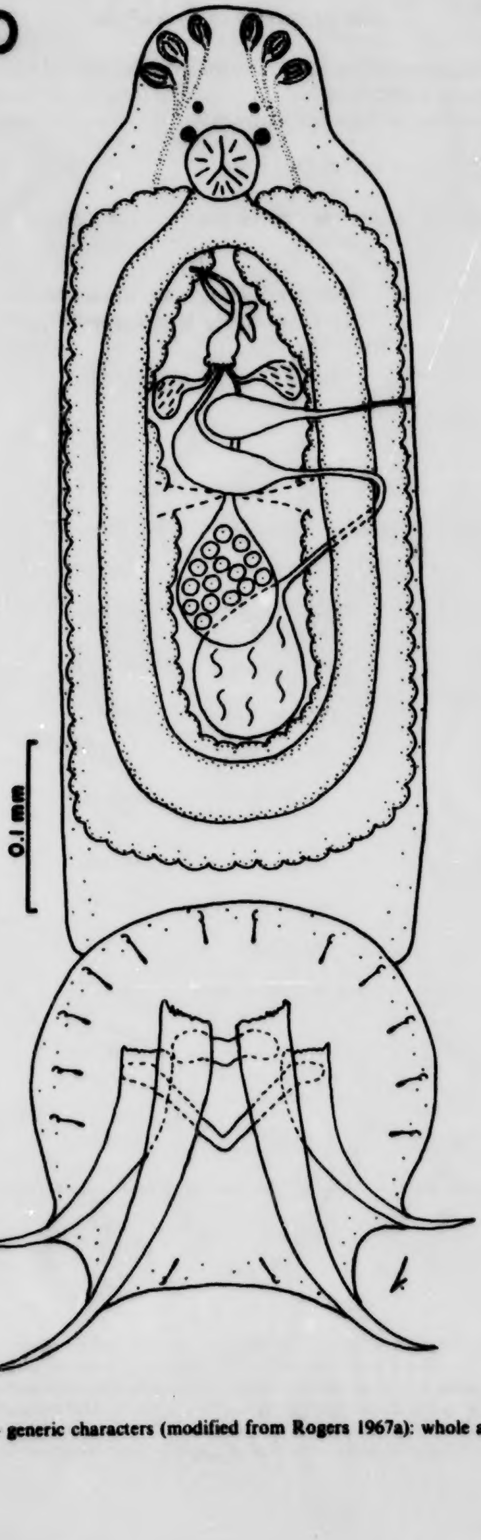

FIG. 11:0. *Lyrodiscus* — generic characters (modified from Rogers 1967a): whole animal, ventral view.

Key to species of *Lyrodiscus*

1 Ventral hamuli markedly longer (more than 100) than dorsal; dorsal hamuli 242–270 long, ventral hamuli 348–390 long; penis 63–82 long .... *L. longibasus* Rogers, 1967 (Fig. 11:1, Table 6)

On fins and body surface of *Lepomis macrochirus* (1); *Pomoxis annularis* (1,2); *P. nigromaculatus* (1,2)
Records: 1. Dechtiar 1972b (Ont); 2. 1973 (Ont)

Ventral hamuli not markedly longer (not more than 25) than dorsal 2

2 Body length less than 750; hamuli comparatively small: dorsal hamuli up to 126 long, ventral hamuli up to 134 long .... *L. minimus* Kritsky and Hathaway, 1969 (Fig. 11:2, Table 6)

On fins of *Ambloplites rupestris*
Record: Dechtiar 1973 (Ont)

Body length more than 1100 3

TABLE 6. Comparative measurements (in μm) of the species of *Lyrodiscus* Rogers, 1967, recorded from fishes of Canada (from Dechtiar 1973).

Species	*L. longibasus*	*L. minimus*	*L. rupestris*	*L. seminolensis*
Body: length	1942 (1411–2339)	625 (361)[a]	1340 (1208–1604)	1302 (1132–1509)
width	323 (264–443)	100	213 (189–273)	281 (235–311)
Dorsal hamuli: length	256 (242–270)	126 (83)[a]	214 (188–269)	138 (126–149)
Dorsal bar: transverse length	122 (108–138)	124 (65)[a]	126 (123–138)	108 (102–117)
Ventral hamuli: length	380 (348–390)	134 (90)[a]	223 (174–290)	149 (125–158)
Ventral bar: transverse length	95 (90–101)	60 (55)[a]	75 (69–96)	55 (50–57)
width	(31–34)[b]	13	30 (26–36)	22 (21–24)
Marginal hooks: length	30 (26–32)	16 (15)[a]	20 (19–21)	30 (29–32)
Penis: length	71 (63–82)	56 (39)[a]	56 (43–62)	111 (95–129)
Accessory piece: length	54 (47–63)	27 (27)[a]	31 (23–41)	66 (62–72)
Site(s)	fins & body surface	fins	nasal cavities, fins & body surface	fins & body surface
Host(s)	*Lepomis macrochirus* *Pomoxis annularis* *P. nigromaculatus*	*Ambloplites rupestris*	*Ambloplites rupestris*	*Lepomis macrochirus*
Locality	Ontario	Ontario	Ontario	Ontario

[a] From Kritsky and Hathaway (1969).
[b] This value was quoted by Dechtiar (1973) to be 30 (31–34); the mean value is considered to be a typographical error.

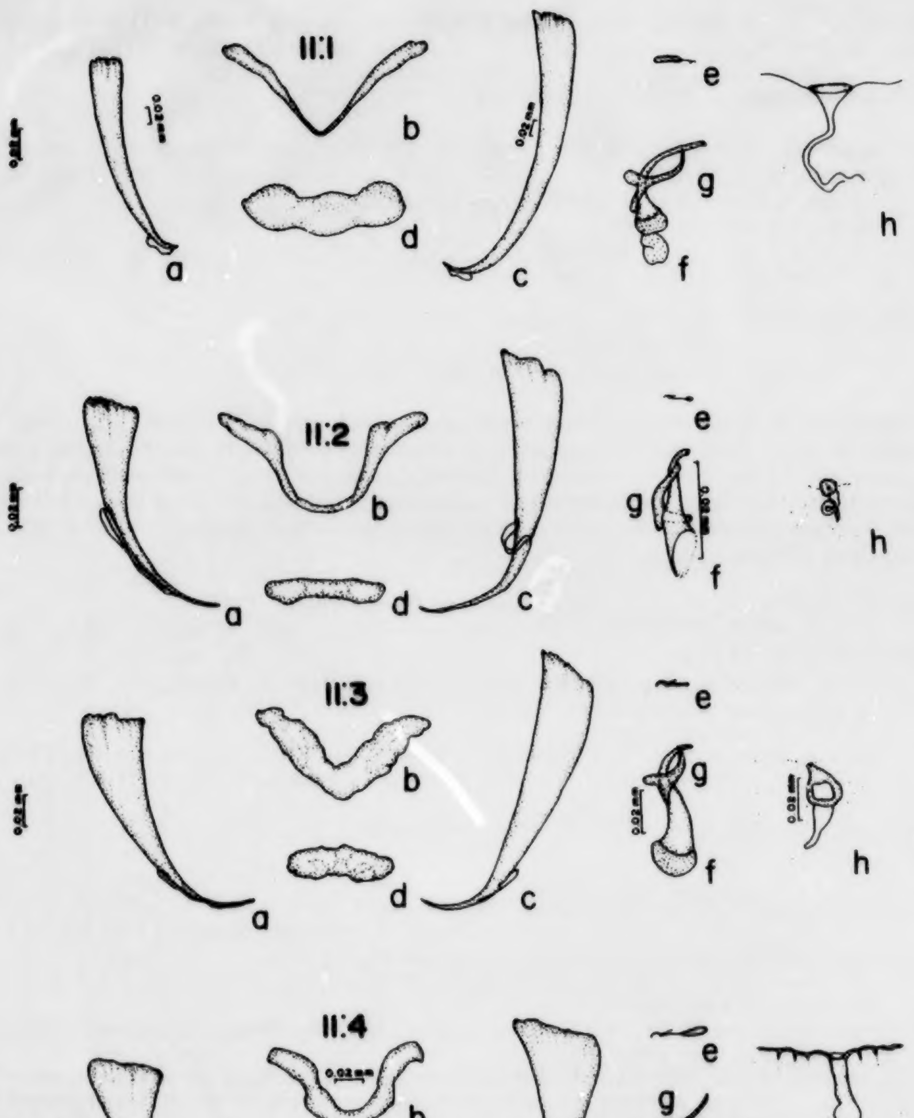
II:1
0.02 mm
a
b
c
d
e
f
g
h
II:2
0.02 mm
a
b
c
d
e
f
g
h
II:3
0.02 mm
a
b
c
d
e
f
g
h
II:4
0.02 mm
a
b
c
d
e
f
g
h

FIG. 11:1–11:4. *Lyrodiscus* spp. 11:1. *L. longibasus* (redrawn from Dechtiar 1973): a. dorsal hamulus; b. dorsal bar; c. ventral hamulus; d. ventral bar; e. marginal hook; f. penis; g. accessory piece; h. vagina. 11:2 *L. minimus* (a–e, h redrawn from Dechtiar 1973, f and g modified from Kritsky and Hathaway 1969): a. dorsal hamulus; b. dorsal bar; c. ventral hamulus; d. ventral bar; e. marginal hook; f. penis; g. accessory piece; h. vagina. 11:3 *L. rupestris* (redrawn from Dechtiar 1973): a. dorsal hamulus; b. dorsal bar; c. ventral hamulus; d. ventral bar; e. marginal hook; f. penis; g. accessory piece; h. vagina. 11:4 *L. seminolensis* (redrawn from Dechtiar 1973): a. dorsal hamulus; b. dorsal bar; c. ventral hamulus; d. ventral bar; e. marginal hook; f. penis; g. accessory piece; h. vagina.

3 **Dorsal hamuli 188–269 long, ventral hamuli 174–290 long; marginal hooks 19–21. Penis comparatively short, 43–62** .... ***L. rupestris* Dechtiar, 1973 (Fig. 11:3, Table 6)**

In nasal cavities, on fins and body surface of *Ambloplites rupestris*
Records: Dechtiar 1972b (Ont); 1973 (Ont)

Dorsal hamuli 126–149 long, ventral hamuli 125–158 long; marginal hooks 29–32 long. Penis comparatively long, 95–129 .... *L. seminolensis* Rogers, 1967 (Fig. 11:4, Table 6)

On fins, body surface of *Lepomis macrochirus*
Record: Dechtiar 1973 (Ont)

Records of unidentified *Lyrodiscus* sp. are listed from:

Lepomis macrochirus, *Pomoxis nigromaculatus* — Dechtiar 1972b, Ontario.

Onchocleidus Mueller, 1936 (Fig. 12:0)

Ancyrocephalidae: two pairs of hamuli (one dorsal, one ventral); transverse bars not articulating with each other; marginal hooks dissimilar in shape and size. Copulatory complex (Type 2) comprising sclerotized, tubular penis with inflated base and two spiral filaments; accessory piece variable with proximal aperture through which distal tip of penis protrudes. Vagina sclerotized or not, on right side of body, leading to seminal receptacle. Vitellaria coextensive with intestine, extending laterally to body margin. On gills of North American freshwater fishes (Centrarchidae).

Key to species of *Onchocleidus*

1 Penis more than 70 long ....
.... *O. chautauquaensis* (Mueller, 1938) Murith and Beverley-Burton, 1984 (Fig. 12:2, Table 7)

Syn: *Urocleidus chautauquaensis* (Mueller, 1938)
On gills of *Ambloplites rupestris*
Records: Dechtiar 1972b (Ont); Hanek and Fernando 1973a (Ont); 1973b (Ont); 1974 (Ont); Molnar et al. 1974 (Ont); Hanek 1977 (Ont); Hanek and Fernando 1978a (Ont); 1978e (Ont)

Penis less than 70 long 2

2 Penis 25–34 long; accessory piece lightly sclerotized, tent-like ....
.... *O. similis* Mueller, 1936 (Fig. 12:8, Table 7)

Syn: *Urocleidus similis* (Mueller, 1936) Mizelle and Hughes, 1938
Urocleidus procax Mizelle and Donahue, 1944 (new syn.)
On gills of *Lepomis gibbosus*
Records: Dechtiar 1972b (Ont); Cone and Anderson 1977 (Ont); Beverley-Burton and Suriano 1981 (Ont); Cone 1980 (NB)
Remarks: Beverley-Burton and Suriano (1981) recognized *Onchocleidus* as a valid genus, redescribed *O. similis*, and suggested that *U. procax* might prove to be a synonym. A comparison of data based on a recent study of the type material of *U. procax* and the specimens of *O. similis* described by Beverley-Burton and Suriano (1981) shows the two forms are identical. Thus *U. procax* is considered a synonym of *O. similis*.

Penis 36–65 long; accessory piece tent-like or almost rectangular with proximal aperture 3

12:0

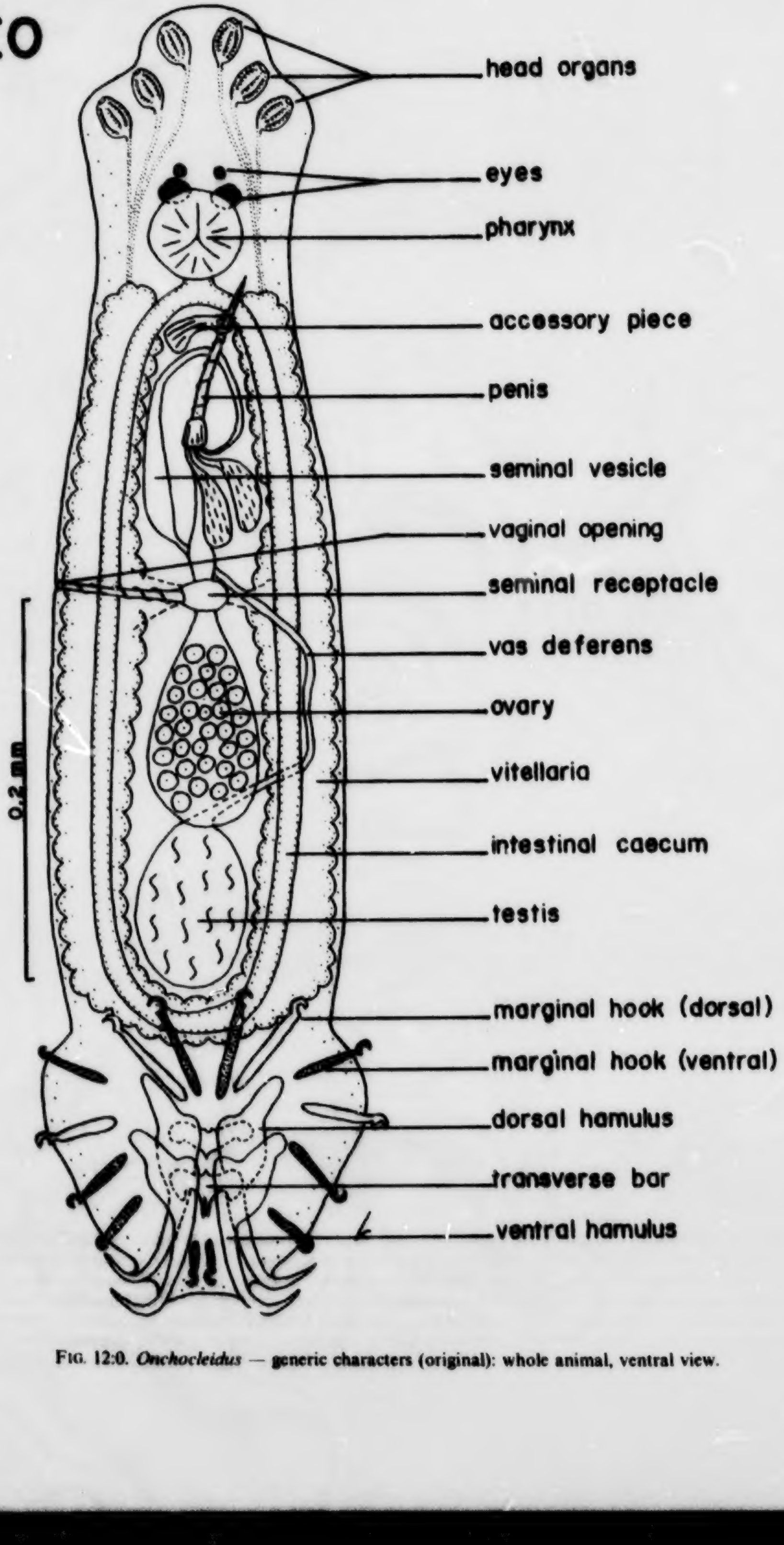
head organs
eyes
pharynx
accessory piece
penis
seminal vesicle
vaginal opening
seminal receptacle
vas deferens
ovary
vitellaria
intestinal caecum
testis
marginal hook (dorsal)
marginal hook (ventral)
dorsal hamulus
transverse bar
ventral hamulus
0,2 mm

FIG. 12:0. *Onchocleidus* — generic characters (original): whole animal, ventral view.

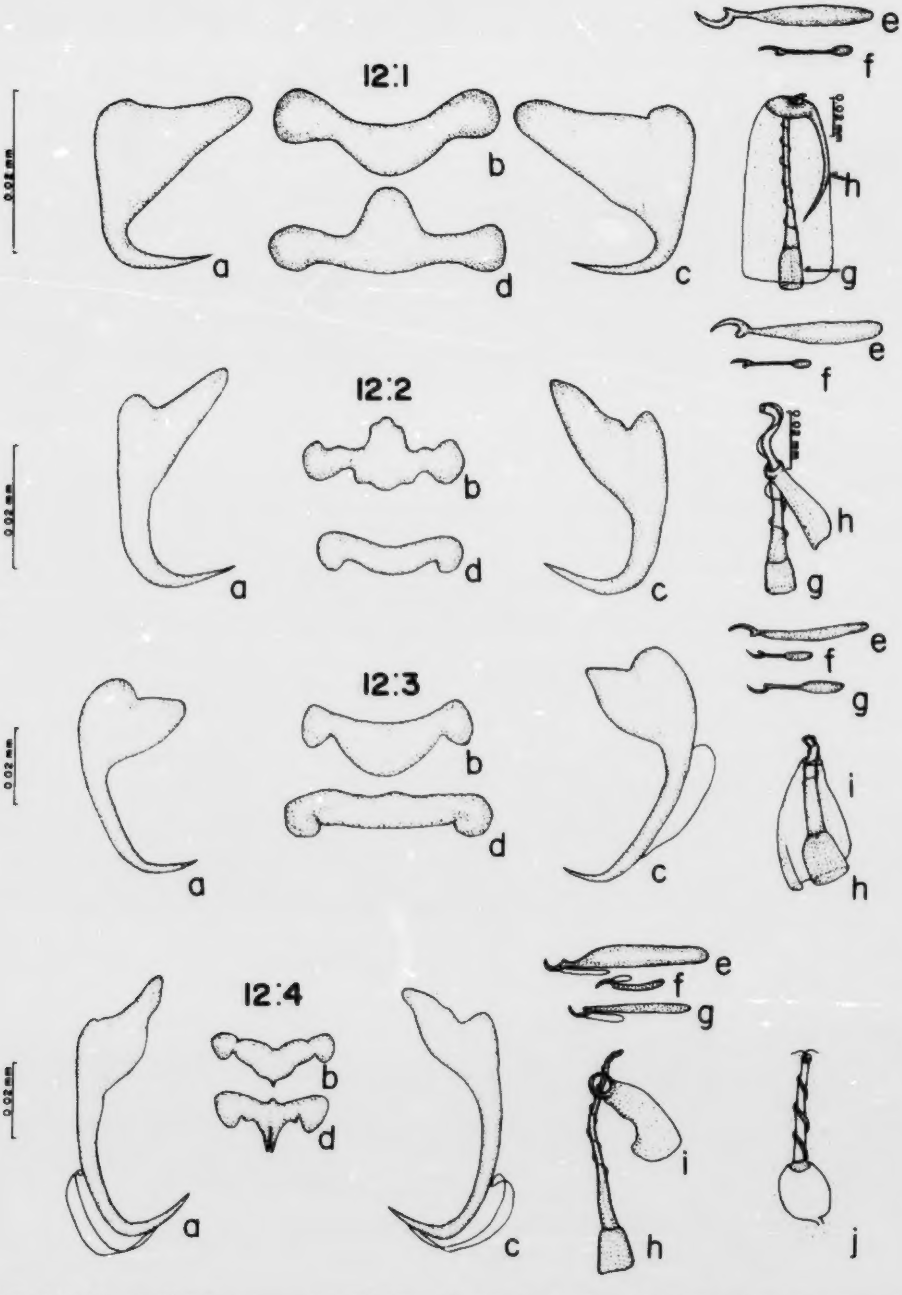

FIG. 12:1–12:4. *Onchocleidus* spp. 12:1 *O. attenuatus* (modified from Mizelle 1941): a. dorsal hamulus; b. dorsal bar; c. ventral hamulus; d. ventral bar; e. marginal hooks I, III–VII; f. marginal hook II; g. penis; h. accessory piece. 12:2. *O. chautauquaensis* (a–e, g, h modified from Mueller 1938, f from Mizelle and Regensberger 1945): a. dorsal hamulus; b. dorsal bar; c. ventral hamulus; d. ventral bar; e. marginal hooks I, III–VII; f. marginal hook II; g. penis; h. accessory piece. 12:3. *O. chrysops* (modified from Mizelle and Klucka 1953): a. dorsal hamulus; b. dorsal bar; c. ventral hamulus; d. ventral bar; e. marginal hook I; f. marginal hook II; g. marginal hook III–VII; h. penis; i. accessory piece. 12:4. *O. ferox* (redrawn from Beverley-Burton and Suriano 1981): a. dorsal hamulus; b. dorsal bar; c. ventral hamulus; d. ventral bar; e. marginal hook I; f. marginal hook II; g. marginal hook VII; h. penis; i. accessory piece; j. vagina.

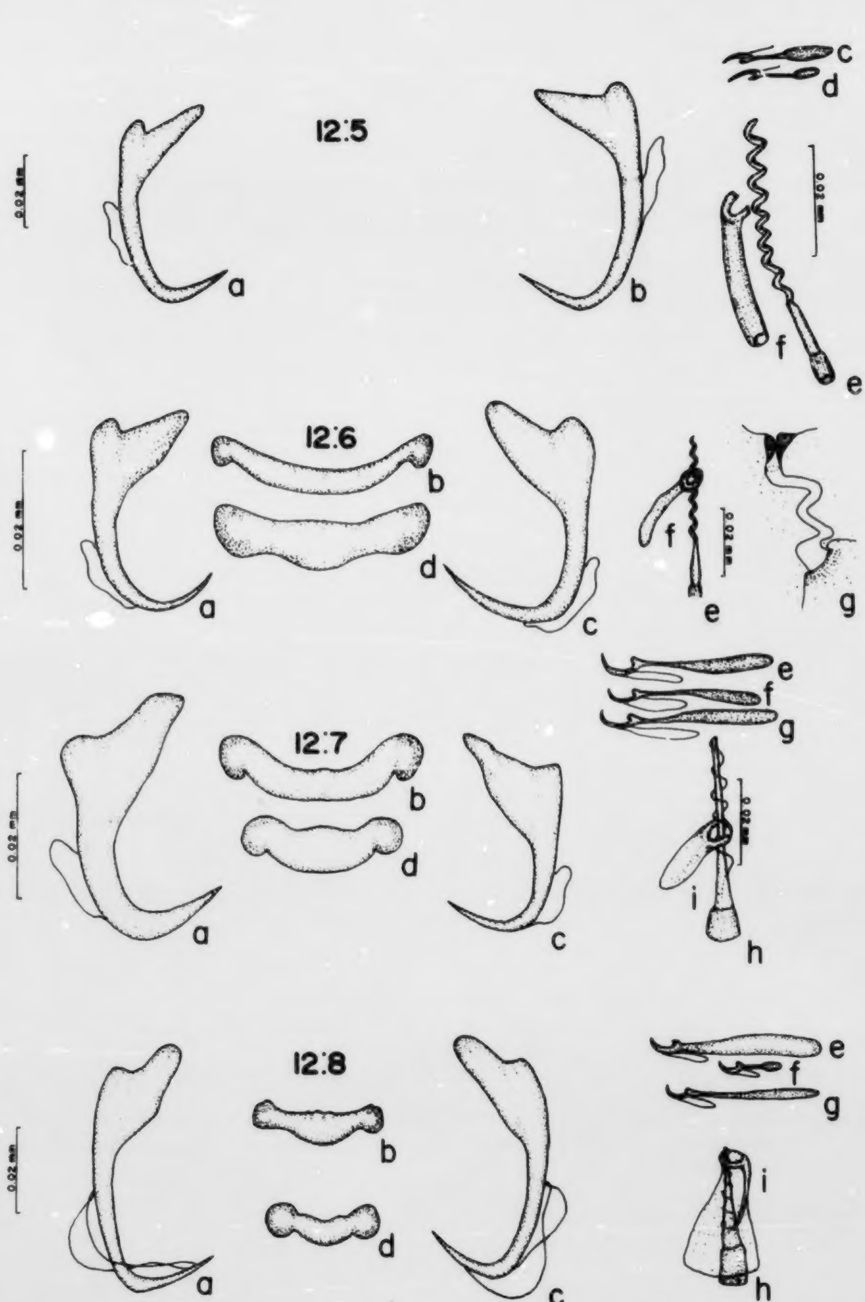

FIG. 12:5–12:8. *Onchocleidus* spp. 12:5. *O. helicis* (modified from Mizelle and Regensberger 1945): a. dorsal hamulus; b. ventral hamulus; c. marginal hooks I, III–VII; d. marginal hook II; e. penis; f. accessory piece (figures of bars not available). 12:6. *O. principalis* (modified from Mizelle 1936): a. dorsal hamulus; b. dorsal bar; c. ventral hamulus; d. ventral bar; e. penis; f. accessory piece; g. vagina (figures of marginal hooks not available). 12:7. *O. rogersi* (modified from Hanek and Fernando 1972a): a. dorsal hamulus; b. dorsal bar; c. ventral hamulus; d. ventral bar; e. marginal hook I; f. marginal hook II; g. marginal hook III–VII; h. penis; i. accessory piece. 12:8. *O. similis* (redrawn from Beverley-Burton and Suriano 1981): a. dorsal hamulus; b. dorsal bar; c. ventral hamulus; d. ventral bar; e. marginal hook I; f. marginal hook II; g. marginal hook III; h. penis; i. accessory piece.

3 Hamuli more than 50 long 4

Hamuli less than 50 long 5

4 Vagina conspicuous with sclerotized spiral thickening of wall; transverse bars 25–32 transverse length, both with median, posterior extension .... *O. ferox* (Mueller, 1934) Mueller, 1936 (Fig. 12:4, Table 7)

Syn: *Urocleidus ferox* Mueller, 1934
On gills of *Lepomis gibbosus* (1,2,3,4,5,6,7); *L. macrochirus* (2); *Micropterus dolomieui* (2)
Records: 1. Mizelle and Donahue 1944 (Ont); 2. Hanek and Fernando 1972a (Ont); 3. Dechtiar 1973 (Ont); 4. Hanek and Fernando 1978a (Ont); 5. 1978b (Ont); 6. 1978d (Ont); 7. Beverley-Burton and Suriano 1981 (Ont)
Remarks: Beverley-Burton and Suriano (1981) recognized *Onchocleidus* as a valid genus and redescribed *O. ferox*.

Vagina inconspicuous; transverse bars 46–65 transverse length, lacking median, posterior extension .... *O. chrysops* (Mizelle and Klucka, 1953) n. comb. (Fig. 12:3, Table 7)

Syn: *Urocleidus chrysops* Mizelle and Klucka, 1953
On gills of *Morone chrysops*
Record: Dechtiar 1972b (Ont)
Remarks: Beverley-Burton and Suriano (1981) included *U. chrysops* in a list of species with a "*ferox*-type" penis and noted its possible inclusion in *Onchocleidus*. Thus, *O. chrysops* n. comb. is proposed.

5 Hamuli with large, almost triangular basal region; shaft and point short. Vagina conspicuous .... *O. attenuatus* (Mizelle, 1941) n. comb. (Fig. 12:1, Table 7)

Syn: *Urocleidus attenuatus* Mizelle, 1941
On gills of *Lepomis gibbosus*
Records: Hanek and Fernando 1973a (Ont); 1975 (Ont); 1978a (Ont); 1978d (Ont)
Remarks: Beverley-Burton and Suriano (1981) included *U. attenuatus* in a list of species with a "*ferox* type" penis and noted its possible inclusion in *Onchocleidus*. Thus, *O. attenuatus* n. comb. is proposed.

Hamuli with basal region not unduly large or triangular; shaft distinct, elongate, narrow. Vagina inconspicuous[29] 6

6 Body 948–1164 long. On *Morone americana* .... *O. rogersi* (Hanek and Fernando, 1972) n. comb. (Fig. 12:7, Table 7)

Syn: *Urocleidus rogersi* Hanek and Fernando, 1972
On gills of *Morone americana*
Record: Hanek and Fernando 1972a (Ont)
Remarks: Beverley-Burton and Suriano (1981) included *U. rogersi* in a list of species with a "*ferox* type" penis and noted its possible inclusion in *Onchocleidus*. Thus, *O. rogersi* n. comb. is proposed.

Body 234–660 long. On *Micropterus* spp. 7

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[29] From a study of the literature and deposited type material.

TABLE 7. Comparative measurements (in μm) of the species of *Onchocleidus* Mueller, 1936, recorded from fishes of Canada.

Species	*O. attenuatus*	*O. chautauquaensis*	*O. chrysops*	*O. ferox*	*O. helicis*	*O. principalis*	*O. rogersi*	*O. similis*
Source of data	Hanek and Fernando (1973a)	Hanek and Fernando (1973a)	Mizelle and Klucka (1953)	Beverley-Burton and Suriano (1981)	Mizelle and Regensberger (1945)	Hanek and Fernando (1972a)	Hanek and Fernando (1972a)	Beverley-Burton and Suriano (1981)
Body: length width	897–1222 156–195	1203–1460 183–224	609 (585–666) 115 (99–141)	329 (250–402) 76 (61–94)	234–306 77–95	480–660[b] 84–132	1044 (948–1164) 204 (144–252)	280 (190–350) 78 (60–100)
Dorsal hamuli: length	30–33	34–36	59 (58–60)	67 (61–72)	36–41	25–37	38 (36–39)	55 (48–61)
Dorsal bar: transverse length	25–27	23–25	46[a]	29 (25–32)	40	29–35	34 (33–36)	26 (24–28)
Ventral hamuli: length	25–28	34–36	65 (62–69)	67 (65–70)	41–43	30–32[c]	31 (29–32)	56 (50–61)
Ventral bar: transverse length	25–27	22–24	53 (49–56)	29 (25–30)	38	28–33	25 (23–25)	28 (25–30)
Marginal hooks I, III–VII: length II: length	20–23 13–15	27–33 12–14	25–36 18	27–45 14 (13–16)	20–23 14–16	17–24 14–15	27–30 26 (25–26)	24–31 11 (10–12)
Penis: length	58–65	72–78	40	55 (46–60)	36–41	44–51	45 (40–51)	31 (25–34)
Accessory piece: length	38–43	32–35	28 (27–29)	35 (31–39)	27–29	21–27	22 (19–26)	22 (20–24)
Site	gills	gills	gills	gills	gills	gills	gills	gills
Host(s)	*Lepomis gibbosus* *L. macrochirus* *Micropterus dolomieui*	*Ambloplites rupestris*	*Morone chrysops*	*Lepomis gibbosus* *L. macrochirus* *Micropterus dolomieui*	*Micropterus salmoides*	*Micropterus dolomieui* *M. salmoides*	*Morone americana*	*Lepomis gibbosus*
Locality(ies)	Ontario	Ontario	Ontario	Ontario	Ontario	Ontario	Ontario	New Brunswick Ontario

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[a] Range not stated.

[b] Morphometric data from *M. dolomieui* and *M. salmoides* combined.

[c] Hanek and Fernando (1972a) gave the length of the ventral hamulus of worms from *M. dolomieui* as 15–19, which may be a typographical error. Thus, 30–32 is the value quoted for specimens from *M. salmoides* only.

13:0

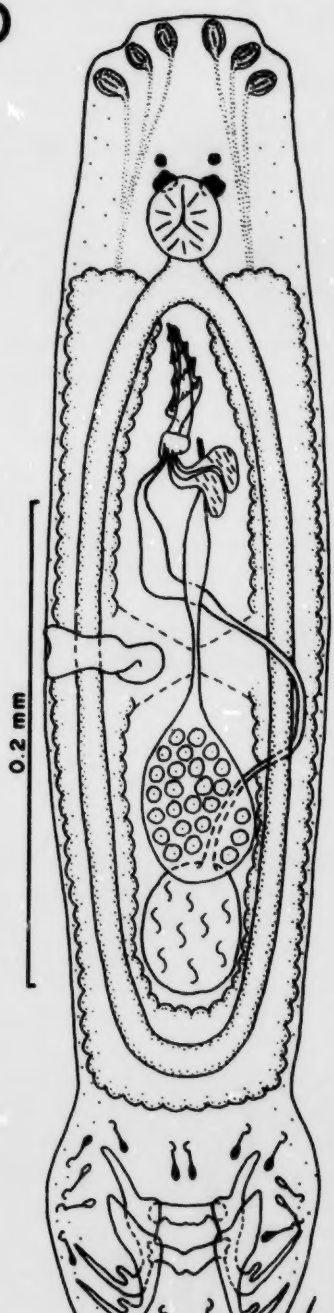

FIG. 13:0. *Pterocleidus* — generic characters (original): whole animal, ventral view.

7 Dorsal bar 40 transverse length with posterior, median spine;[30] ventral bar 38 transverse length. Penis 36–41 long .... *O. helicis* Mueller, 1936 (Fig. 12:5, Table 7)

Syn: *Urocleidus helicis* (Mueller, 1936) Mizelle and Hughes, 1938
On gills of *Micropterus salmoides*
Record: Dechtiar 1972b (Ont)
Remarks: Although the descriptions of *O. helicis* provided by Mueller (1936a) and Mizelle and Regensberger (1945) are inadequate, the species cannot be accommodated in the genus *Urocleidus* (see Beverley-Burton and Suriano 1981). Thus, this species is reinstated in *Onchocleidus* as originally designated by Mueller (1936a).

Dorsal bar 29–35 transverse length, lacking posterior, median spine; ventral bar 28–33 transverse length. Penis 44–51 long .... *O. principalis* Mizelle, 1936 (Fig. 12:6, Table 7)

Syn: *Urocleidus principalis* (Mizelle, 1936) Mizelle and Hughes, 1938
On gills of *Micropterus dolomieui* (1); *M. salmoides* (1,2)
Records: 1. Hanek and Fernando 1972a (Ont); 2. Molnar et al. 1974 (Ont)
Remarks: Beverley-Burton and Suriano (1981) included *U. principalis* in a list of species with a "*ferox* type" penis and noted its possible inclusion in *Onchocleidus*. Thus, this species is reinstated in *Onchocleidus* as originally designated by Mizelle (1936).

Pterocleidus Mueller, 1937 (Fig. 13:0)

Ancyrocephalidae: two pairs of hamuli (one dorsal, one ventral), each with flat finger-like projection on inner curve of blade; transverse bars not articulating with each other; marginal hooks of similar shape but slightly different size. Copulatory complex (Type 2) comprising sclerotized, tubular penis, with inflated base and two spiral filaments supporting voluminous sheath; accessory piece inconspicuous, incorporated into penis sheath. Vagina lightly sclerotized, opening on right side of body, leading to seminal receptacle. Vitellaria coextensive with intestine and extending laterally to body margin. On gills of North American freshwater fishes (Centrarchidae). One species on Canadian fishes.

Pterocleidus acer (Mueller, 1936) Mueller, 1937 (Fig. 13:1)

Morphometric data in Table 8.

Syn: *Urocleidus acer* (Mueller, 1936) Mizelle and Hughes, 1938
On gills of *Lepomis gibbosus*
Records: Hanek and Fernando 1972a (Ont); 1978a (Ont); 1978d (Ont); Beverley-Burton and Suriano 1980b (Ont); 1980c (Ont)
Remarks: Beverley-Burton and Suriano (1980b) recognized *Pterocleidus* as a valid genus and redescribed *P. acer*.

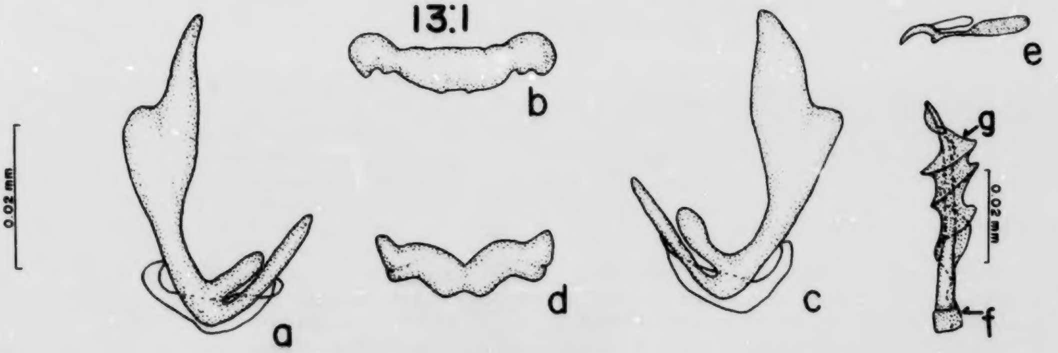

FIG. 13:1. *Pterocleidus acer* (redrawn from Beverley-Burton and Suriano 1980b): a. dorsal hamulus; b. dorsal bar; c. ventral hamulus; d. ventral bar; e. marginal hook; f. penis; g. accessory piece.

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[30] From text description in Mizelle and Regensberger (1945).

14:0

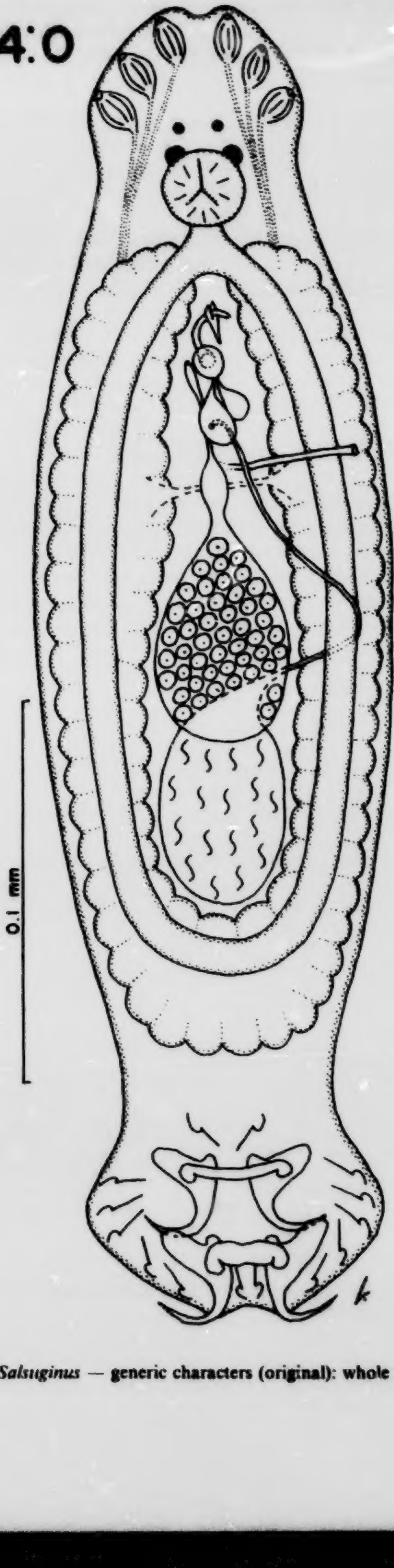

FIG. 14:0. *Salsuginus* — generic characters (original): whole animal, ventral view.

Salsuginus n. g.[31] (Fig. 14:0)

Ancyrocephalidae: two pairs of hamuli (one dorsal, one ventral); transverse bars not articulating with each other; marginal hooks of similar shape and size. Copulatory complex (Type 3) comprising sclerotized, strongly curved, tubular penis with inflated base; accessory piece variable. Vagina nonsclerotized, opening on left side of body, leading to seminal receptacle.[32] Vitellaria coextensive with intestine, extending laterally to body margin. On gills of North American freshwater fishes (Cyprinodontidae).

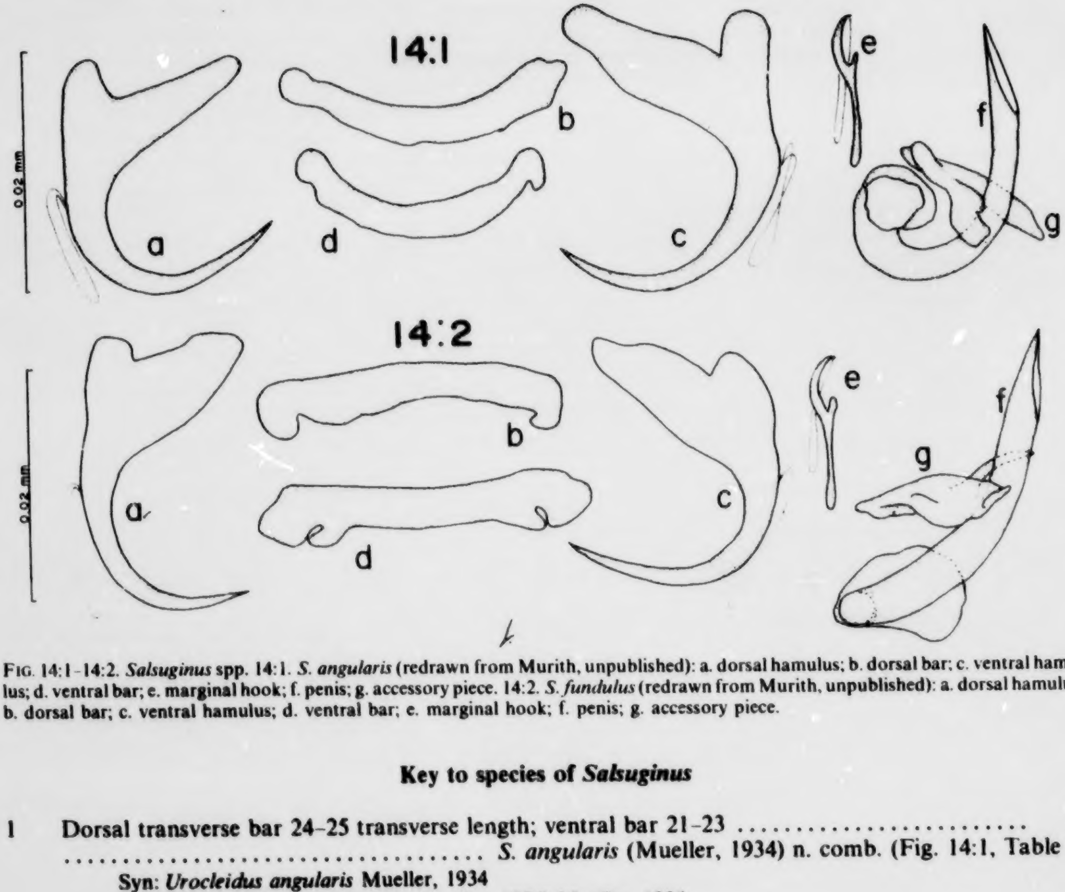

FIG. 14:1–14:2. *Salsuginus* spp. 14:1. *S. angularis* (redrawn from Murith, unpublished): a. dorsal hamulus; b. dorsal bar; c. ventral hamulus; d. ventral bar; e. marginal hook; f. penis; g. accessory piece. 14:2. *S. fundulus* (redrawn from Murith, unpublished): a. dorsal hamulus; b. dorsal bar; c. ventral hamulus; d. ventral bar; e. marginal hook; f. penis; g. accessory piece.

Key to species of *Salsuginus*

1 Dorsal transverse bar 24–25 transverse length; ventral bar 21–23 ....
.... *S. angularis* (Mueller, 1934) n. comb. (Fig. 14:1, Table 8)

Syn: *Urocleidus angularis* Mueller, 1934
Ancyrocephalus angularis (Mueller, 1934) Mueller, 1936
Cleidodiscus angularis Mueller, 1934 of Wiles, 1975
On gills of *Fundulus diaphanus* (2,3,4); *F. heteroclitus* (1)
Records: 1. Dickinson and Threlfall 1975 (Nfld); 2. 1976 (Nfld); 3. Wiles 1975 (NS); 4. Murith 1983 (pers. comm.) (Ont)
Remarks: Beverley-Burton and Suriano (1980a) and Suriano and Beverley-Burton (1981) provided emended diagnoses for *Cleidodiscus* and *Urocleidus*, respectively. From a study of paratype material from Mueller's collection it is evident that, because of distinct differences in copulatory complex and haptoral sclerites, this species cannot be included in either of the above genera. Thus *Salsuginus* n. g. is proposed with *S. angularis* n. comb. as type species.

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[31] See Murith and Beverley-Burton (1985).

[32] Based on observations of living specimens of an undescribed species parasitic on *Fundulus* sp. from Bermuda. Further studies are in progress to confirm this feature (Murith, pers. comm.).

Dorsal transverse bar 28–29 transverse length; ventral bar 29–30 .... *S. fundulus* (Mizelle, 1940) n. comb. (Fig. 14:2, Table 8)

Syn: *Urocleidus fundulus* Mizelle, 1940

On gills of *Fundulus diaphanus*

Records: Hanek and Fernando 1972a (Ont); Cone 1980 (NB)

Remarks: *Salsuginus fundulus* was originally described from material found on *Fundulus catenatus* taken in Tennessee, U.S.A. (Mizelle 1940). Studies in progress, involving a large collection of *Salsuginus* sp. from *Fundulus diaphanus* taken in Ontario, give rise to the suggestion that only one species occurs on this host in Canada and this is considered to be *Salsuginus angularis* (Murith, pers. comm.). However, until fresh material from *Fundulus catenatus* (which does not occur in Canada) is examined it is impossible to comment on the status of *Salsuginus fundulus* or on the above record from Canada.

TABLE 8. Comparative measurements (in μm) of the species of *Pterocleidus* Mueller, 1937, and *Salsuginus* n. g. recorded from fishes of Canada.

Species	*P. acer*	*S. angularis*	*S. fundulus*
Source of data	Beverley-Burton and Suriano (1980b)	Murith (1983, pers. comm.[c])	Murith (1983, pers. comm.[e])
Body: length	560 (500–700)	301 (232–426)	315 (290, 340)
width	125 (100–150)	88 (61–124)	137 (119, 155)
Dorsal hamuli: length	42 (38–45)	20 (19–21)	25 (24–26)
Dorsal bar: transverse length	28 (25–33)	22 (20–24)	29 (28,30)
Ventral hamuli: length	41 (38–45)	23 (22–24)	25 (23–27)
Ventral bar: transverse length	29 (28–30)	22 (20–24)	29 (28,31)
Marginal hooks: length	20 (18–25)[a] 11 (10–12)[b]	13 (12–13)	13 (11–14)
Penis: length	55 (50–58)	35 (30–38)[d]	41 (40, 41)[d]
Accessory piece: length	—	17 (14–20)	15(?)
Site	gills	gills	gills
Host(s)	*Lepomis gibbosus*	*Fundulus diaphanus* *F. heteroclitus*	*Fundulus diaphanus*
Locality(ies)	Ontario	Newfoundland Nova Scotia	New Brunswick Ontario

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[a] Pairs I, III–VII.

[b] Pair II.

[c] From paratypes found on *F. diaphanus*, deposited by Mueller (1934).

[d] Measured along whole length of curve.

[e] From paratypes found on *F. catenatus*, deposited by Mizelle (1940).

Tetracleidus Mueller, 1936 (Fig. 15:0)

Ancyrocephalidae: haptor small, two pairs of hamuli (one dorsal, one ventral); transverse bars not articulating with each other; marginal hooks of similar shape but slightly different size. Copulatory complex (Type 6) comprising sclerotized, tubular penis with inflated base; accessory piece, sclerotized, grooved, lying alongside penis. Vagina not sclerotized, on right or left side[33] of body, leading to seminal receptacle. Vitellaria coextensive with intestine, extending laterally to body margin. On gills of North American freshwater fishes (Centrarchidae).

Key to species of *Tetracleidus*

1 Ventral bar with conspicuous median projection on posterior border ....
.... *T. stentor* (Mueller, 1937) n. comb. (Fig. 15:5, Table 9)

Syn: *Cleidodiscus stentor* Mueller, 1937
On gills of *Ambloplites rupestris*
Records: Dechtiar 1972b (Ont); Hanek and Fernando 1972a (Ont); 1973b (Ont); 1974 (Ont); 1978a (Ont); 1978c (Ont); 1978e (Ont); Hanek 1977 (Ont); Molnar et al. 1974 (Ont)
Remarks: Beverley-Burton and Suriano (1980a) provided a revised diagnosis for *Cleidodiscus*. From a study of the original description of *C. stentor* by Mueller (1937) and of type specimens, it is evident that, because of distinct differences in the copulatory complex and haptoral sclerites, this species cannot be included in *Cleidodiscus*. Pending examination of living specimens, *T. stentor* n. comb. is tentatively proposed.

Ventral bar lacking conspicuous median projection 2

TABLE 9. Comparative measurements (in μm) of the species of *Tetracleidus* Mueller, 1936, recorded from fishes of Canada.

Species	*T. banghami*	*T. capax*	*T. glenorensis*	*T. longus*	*T. stentor*
Source of data	Murith and Beverley-Burton (1984)	Hanek and Fernando (1972a)	Hanek and Fernando (1972a)	Mizelle (1936)	Hanek and Fernando (1972a)
Body: length	885 (740–1020)	2040–2700	648 (510–809)	626 (492–713)	660–840
width	320 (250–400)	196–340	120 (85–130)	106 (98–123)	96–132
Dorsal hamuli: length	29 (26–33)	27–32	23 (21–24)	37 (31–46)	31–35
Dorsal bar: transverse length	35 (26–44)	29–30	22 (22–25)	37 (28–42)[a]	27–31
Ventral hamuli: length	32 (28–33)	36–39	44 (42–44)	43 (38–41)	39–42
Ventral bar: transverse length	40 (31–44)	30–32	35 (33–36)	38 (32–42)[a]	28–32
Marginal hooks: total length	15–16	15–19	13–20	9–23[a]	14–22
Penis: length	63 (66–75)	75–80	87 (68–89)	"whip-like tube"[b]	56–59
Accessory piece: length	57 (55–58)	49–54	52 (48–56)	grooved guide	40–42
Site	gills	gills	gills	gills	gills
Host(s)	*Micropterus dolomieui*	*Pomoxis annularis* *P. nigromaculatus*	*Ambloplites rupestris* *Micropterus dolomieui*	*Pomoxis annularis* *P. nigromaculatus*	*Ambloplites rupestris*
Locality(ies)	Manitoba Ontario	Manitoba Ontario	Ontario	Ontario	Ontario

[a] From Mizelle (1938).
[b] In type material penis measures more than 100 μm.

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[33] The vagina of the type species (*T. banghami*) is on the right. In the other species which are tentatively included in *Tetracleidus* the vagina is on the left. Hence, this character may have to be emended, following further studies to verify the generic status of *capax*, *glenorensis*, *longus*, and *stentor*.

15:0

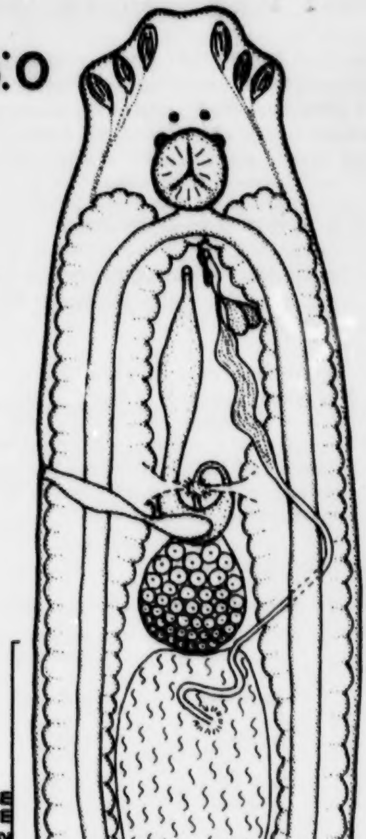
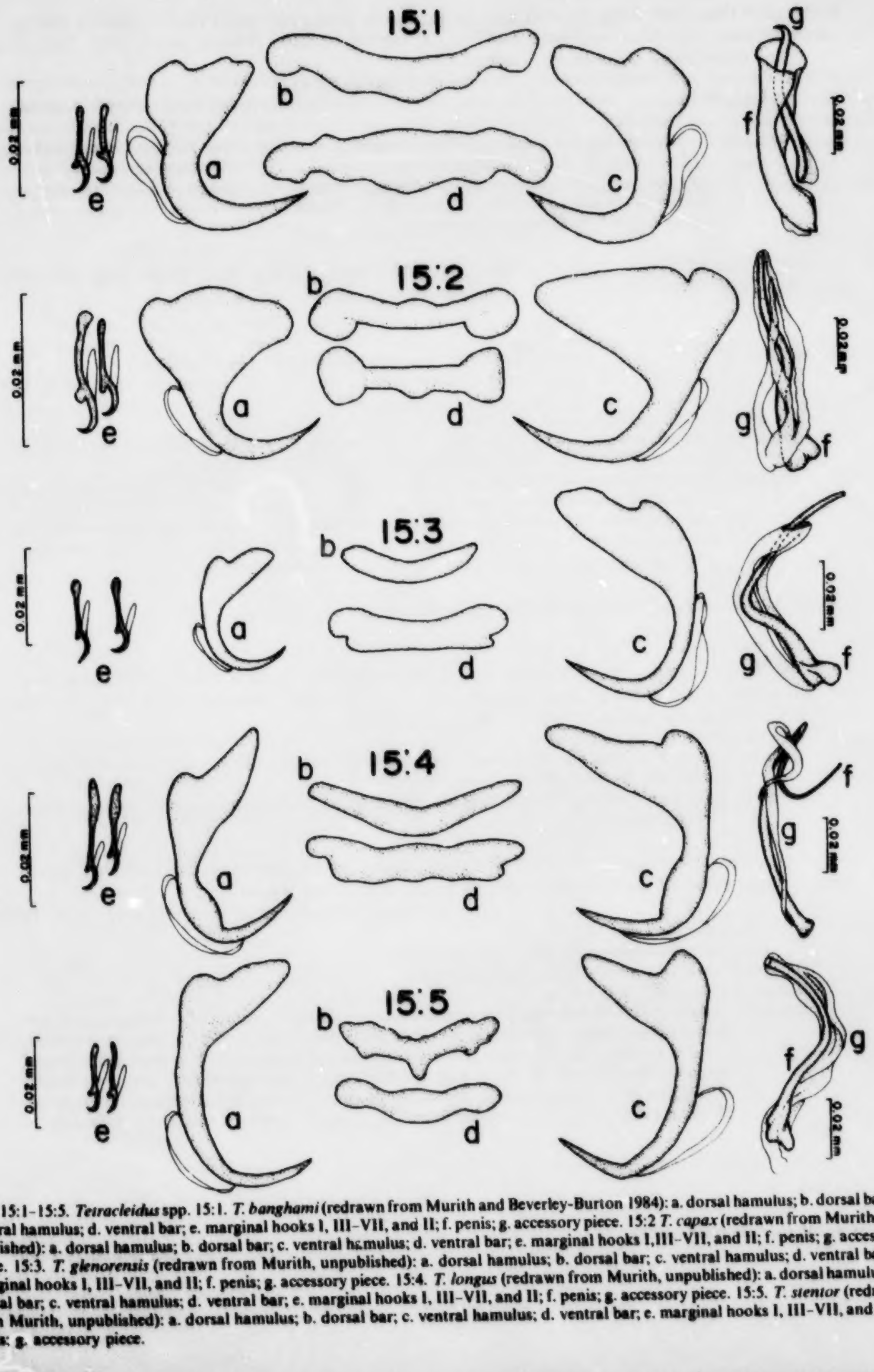


FIG. 15:0. *Tetracleidus* — generic characters (original): whole animal, ventral view.


15:1
a
b
c
d
e
f
g
0.02 mm
0.02 mm
15:2
a
b
c
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e
f
g
0.02 mm
0.02 mm
15:3
a
b
c
d
e
f
g
0.02 mm
0.02 mm
15:4
a
b
c
d
e
f
g
0.02 mm
0.02 mm
15:5
a
b
c
d
e
f
g
0.02 mm
0.02 mm

FIG. 15:1–15:5. *Tetracleidus* spp. 15:1. *T. banghami* (redrawn from Murith and Beverley-Burton 1984): a. dorsal hamulus; b. dorsal bar; c. ventral hamulus; d. ventral bar; e. marginal hooks I, III–VII, and II; f. penis; g. accessory piece. 15:2 *T. capax* (redrawn from Murith, unpublished): a. dorsal hamulus; b. dorsal bar; c. ventral hamulus; d. ventral bar; e. marginal hooks I,III–VII, and II; f. penis; g. accessory piece. 15:3. *T. glenorensis* (redrawn from Murith, unpublished): a. dorsal hamulus; b. dorsal bar; c. ventral hamulus; d. ventral bar; e. marginal hooks I, III–VII, and II; f. penis; g. accessory piece. 15:4. *T. longus* (redrawn from Murith, unpublished): a. dorsal hamulus; b. dorsal bar; c. ventral hamulus; d. ventral bar; e. marginal hooks I, III–VII, and II; f. penis; g. accessory piece. 15:5. *T. stentor* (redrawn from Murith, unpublished): a. dorsal hamulus; b. dorsal bar; c. ventral hamulus; d. ventral bar; e. marginal hooks I, III–VII, and II: f. penis; g. accessory piece.

2 **Body more than 2000 long. Hamuli with large, almost triangular basal region, lacking distinct notch between superficial and deep root ... *T. capax* (Mizelle, 1936) n. comb. (Fig. 15:2, Table 9)**

Syn: *Cleidodiscus capax* Mizelle, 1936
On gills of *Pomoxis annularis* (1); *P. nigromaculatus* (1,2,3,4,)
Records: 1. Dechtiar 1972b (Ont); 2. 1972c (Ont); 3. Hanek and Fernando 1972a (Ont); 4. Lubinsky and Loch 1979 (Man)
Remarks: Beverley-Burton and Suriano (1980a) provided a revised diagnosis for *Cleidodiscus*. From a study of the original description of *C. capax* by Mizelle (1936) and of type specimens, it is evident that, because of distinct differences in the copulatory complex and haptoral sclerites, this species cannot be included in *Cleidodiscus*. Pending examination of living specimens, *T. capax* n. comb. is tentatively proposed.

Body less than 1250 long. Hamuli without triangular basal region, with distinct notch between superficial and deep root 3

3 Dorsal hamuli (21–24 long) markedly shorter than ventral hamuli (42–44 long) .... *T. glenorensis* (Hanek and Fernando, 1972) n. comb. (Fig. 15:3, Table 9)

Syn: *Cleidodiscus glenorensis* Hanek and Fernando, 1972
On gills of *Ambloplites rupestris* (1,2,3,4,5,6,7); *Micropterus dolomieui* (1)
Records: 1. Hanek and Fernando 1972a (Ont); 2. 1973b (Ont); 3. 1974 (Ont); 4. Hanek 1977 (Ont); 5. Hanek and Fernando 1978a (Ont); 6. 1978c (Ont); 7. 1978e (Ont)
Remarks: Beverley-Burton and Suriano (1980a) provided a revised diagnosis for *Cleidodiscus*. From a study of the original description of *C. glenorensis* by Hanek and Fernando (1972a) and of type specimens, it is evident that because of distinct differences in the copulatory complex and haptoral sclerites, this species cannot be included in *Cleidodiscus*. Pending examination of living specimens, *T. glenorensis* n. comb. is tentatively proposed.

Dorsal hamuli only slightly shorter than ventral hamuli 4

4 Penis 66–75 long, comparatively wide; accessory piece grooved with distal hook-like prolongation. Hamuli robust, inner curve of shaft smooth ...... *T. banghami* Mueller, 1936 (Fig. 15:1, Table 9)

Syn: *Cleidodiscus banghami* (Mueller, 1936) Mizelle, 1940
On gills of *Micropterus dolomieui*
Records: Mizelle and Donahue 1944 (Ont); Dechtiar 1972b (Ont); Lubinsky and Loch 1979 (Man); Murith and Beverley-Burton 1984 (Ont)
Remarks: Murith and Beverley-Burton 1984 resurrected *Tetracleidus* and redescribed the type species *T. banghami*.

Penis "whip-like" more than 100 long;[34] accessory piece grooved, closely applied to penis. Hamuli slender, inner curve of shaft irregular due to inflation in distal region .... *T. longus* (Mizelle, 1936) n. comb. (Fig. 15:4, Table 9)

Syn: *Cleidodiscus longus* Mizelle, 1936
Cleidodiscus uniformis Mizelle, 1936 (new syn.)
On gills of *Pomoxis annularis; P. nigromaculatus*
Record: Dechtiar 1972b (Ont)
Remarks: A comparison of data based on a recent study of the type material of *C. longus* and *C. uniformis* shows the two forms are identical (Murith, pers. comm.). Thus, *C. uniformis* is considered a synonym of *C. longus*. Beverley-Burton and Suriano (1980a) provided a revised diagnosis for *Cleidodiscus*. From a study of the original description of *C. longus* by Mizelle (1936) and of type specimens, it is evident this species cannot be included in *Cleidodiscus*. Pending examination of living specimens, *T. longus* n. comb. is tentatively proposed.

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[34] Measurement from type material.

Urocleidus Mueller, 1934 (Fig. 16:0)

Ancyrocephalidae: two pairs of hamuli (one dorsal, one ventral); transverse bars not articulating with each other; marginal hooks of similar shape and size. Copulatory complex (Type 7) comprising sclerotized penis with proximal handle-like region and distal tubular, ejaculatory region; accessory piece with two rami distally fusing to form median hook, and proximally, one or both rami attaching to penis at junction of handle and ejaculatory region. Vagina not observed but presumed ventro-median. Vitellaria coextensive with intestine extending laterally to body margin. On gills of North American freshwater fishes (Percidae and Percopsidae).

Key to species of *Urocleidus*

1 Dorsal hamuli 70–75 long; ventral hamuli 79–93 long. On *Stizostedion* spp. ....
.... *U. aculeatus* (Van Cleave and Mueller, 1932) Mueller, 1934 (Fig. 16:1, Table 10)

On gills of *Stizostedion canadense* (1,2,4); *S. vitreum glaucum* (1); *S. vitreum vitreum* (1,2,3,4,[35]5)
Records: 1. Dechtiar 1972b (Ont); 2. 1972c (Ont); 3. Anthony 1976 (Ont); 4. Lubinsky and Loch 1979 (Man); 5. Suriano and Beverley-Burton 1981 (Ont)

Dorsal hamuli up to 51 long; ventral hamuli up to 55 long 2

TABLE 10. Comparative measurements (in μm) of the species of *Urocleidus* Mueller, 1934, recorded from fishes of Canada.

Species	*U. aculeatus*	*U. adspectus*	*U. baldwini*
Source of data	Suriano and Beverley-Burton (1981)	Cone (1978)	Dechtiar (1974a)
Body: length	780 (750–802)	436–830	547 (519–605)
width	140 (131–150)	120–166	173 (139–188)
Dorsal hamuli: length	73 (70–75)	47–51	41 (31–45)
Dorsal bar: transverse length	45 (40–48)	43–51	30 (23–31)
Ventral hamuli: length	87 (79–93)	51–55	37 (31–42)
Ventral bar: transverse length	38 (35–40)	39–43	27 (21–31)
Marginal hooks: total length	17 (15–20)	17–20	15–21
Penis: length	42 (35–51)	31–38	32 (31–35)
Accessory piece: length	32 (30–35)	—	23 (22–28)
Site	gills	gills	gills
Host(s)	*Stizostedion canadense* *S. vitreum* *S. vitreum vitreum*	*Perca flavescens*	*Percopsis omiscomaycus*
Locality(ies)	Manitoba Ontario	Manitoba New Brunswick Ontario	Ontario

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[35] Subspecies not specified.

16:0

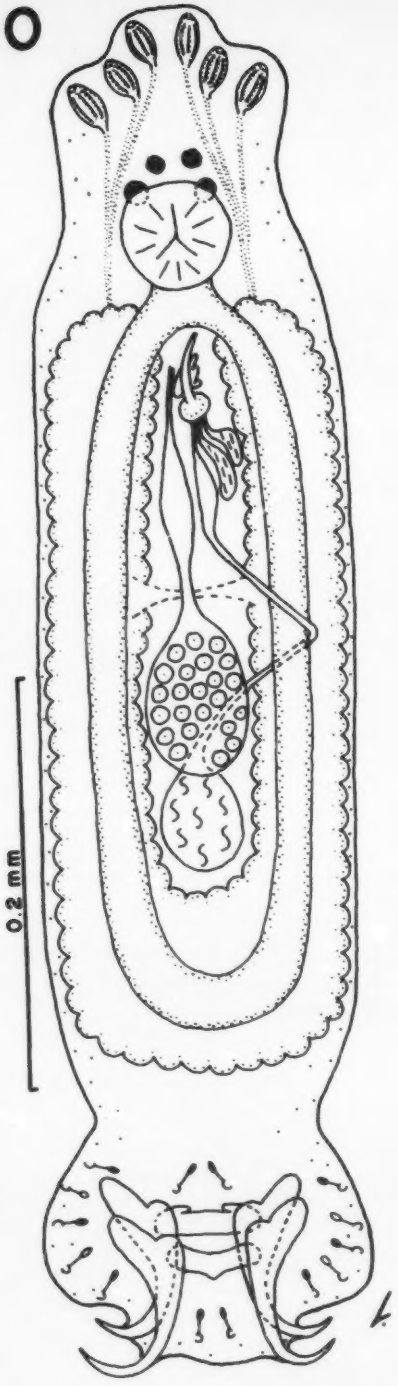
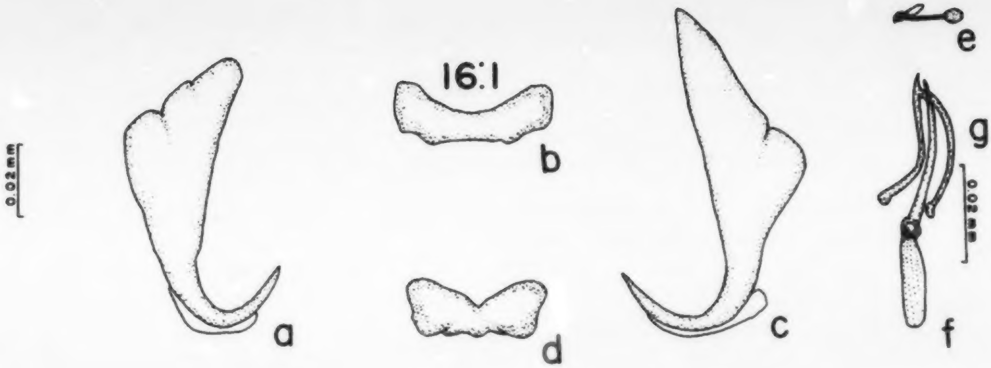


FIG. 16:0. *Urocleidus* — generic characters (original): whole animal, ventral view.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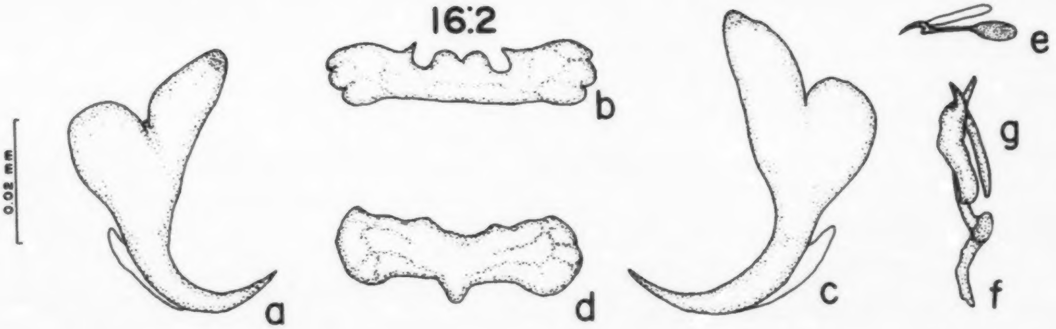
0.02 mm
a
b
c
d
e
f
g
0.02 mm


16:2
0.02 mm
a
b
c
d
e
f
g

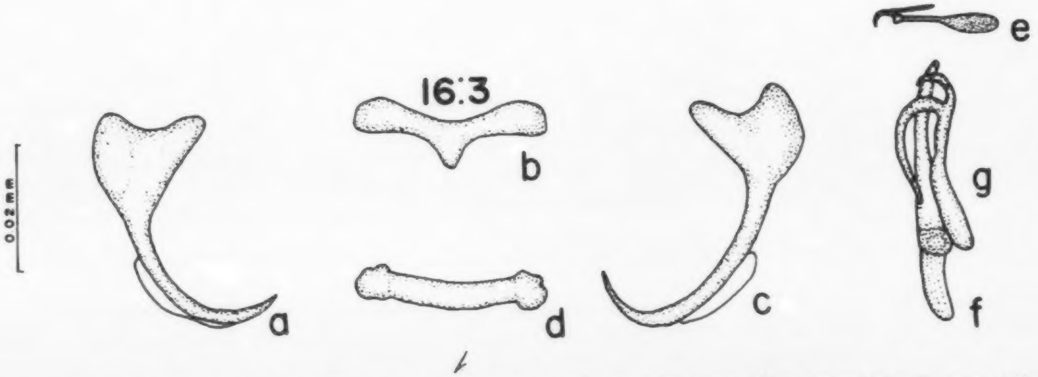

16:3
0.02 mm
a
b
c
d
e
f
g

FIG. 16:1–16:3. *Urocleidus* spp. 16:1. *U. aculeatus* (redrawn from Suriano and Beverley-Burton 1981): a. dorsal hamulus; b. dorsal bar; c. ventral hamulus; d. ventral bar; e. marginal hook; f. penis; g. accessory piece. 16:2. *U. adspectus* (redrawn from Cone 1978): a. dorsal hamulus; b. dorsal bar; c. ventral hamulus; d. ventral bar; e. marginal hook; f. penis; g. accessory piece. 16:3. *U. baldwini* (redrawn from Dechtiar 1974a): a. dorsal hamulus; b. dorsal bar; c. ventral hamulus; d. ventral bar; e. marginal hook; f. penis; g. accessory piece.

2 Dorsal hamuli 47–51 long, ventral hamuli 51–55 long; dorsal bar 43–51 transverse length, ventral bar 39–43 transverse length. On *Perca flavescens* ..... *U. adspectus* Mueller, 1936 (Fig. 16:2, Table 10)

On gills of *Perca flavescens*
Records: Mizelle and Donahue 1944 (Ont); Tedla and Fernando 1969a (Ont); 1970 (Ont); 1972 (Ont); Hanek and Fernando 1972a (Ont); Dechtiar 1972b (Ont); 1972c (Ont); Molnar et al. 1974 (Ont); Cone 1978 (NB); 1979a (NB); 1979b (NB); 1979c (NB); Lubinsky and Loch 1979 (Man); Cone 1980 (NB); Cone and Burt 1981 (NB); 1982a (NB); 1982b (NB)

Dorsal hamuli 31–45 long, ventral hamuli 31–42 long; dorsal bar 23–31 transverse length, ventral bar 21–31 transverse length. On *Percopsis omiscomaycus* .... *U. baldwini* (Dechtiar, 1974) n. comb. (Fig. 16:3, Table 10)

Syn: *Cleidodiscus baldwini* Dechtiar, 1974
On gills of *Percopsis omiscomaycus*
Record: Dechtiar 1974a (Ont)
Remarks: Suriano and Beverley-Burton (1981) noted the similarity of the copulatory apparatus of *C. baldwini* and *U. aculeatus* (Type 7). Thus, *U. baldwini* n. comb. is proposed.

Record of an unidentified *Urocleidus* sp. listed from:

Micropterus salmoides — Molnar et al. 1974, Ontario.
Remarks: It is probable that this designation is incorrect as *Urocleidus* spp. do not appear to parasitize centrarchids.

Records of ancyrocephalid species of uncertain generic affinity — *incertae sedis* (herein listed as Ancyrocephalidae spp.)

"*Ancyrocephalus*" sp. (see Margolis and Arthur 1979)

Fantham and Porter (1948) recorded *Ancyrocephalus* sp. from gills of *Micropterus dolomieui* taken in Nova Scotia. However, as Margolis and Arthur (1979) pointed out, this was probably an incorrect generic identification. Thus, the record is listed under the Ancyrocephalidae.

"*Cleidodiscus*" *vancleavei* Mizelle, 1936 (see Margolis and Arthur, 1979) (Fig. 17:0)

Morphometric data (from Hanek and Fernando 1972a); body 480–696 long by 82–96 wide; dorsal hamuli 35–40 long; dorsal bar 27–29 transverse length; ventral hamuli 38–45 long; ventral bar 24–27 transverse length; marginal hooks 13–24 long; penis 22–25 long, accessory piece 18–21 long.

On gills of *Pomoxis nigromaculatus*
Record: Hanek and Fernando 1972a (Ont)
Remarks: Following the emendation of the generic diagnosis for *Cleidodiscus* of Beverley-Burton and Suriano (1980a) it is clear that *C. vancleavei* cannot be included in this genus. Thus, further studies on living material are required before a generic designation is feasible.

"*Urocleidus*" *alatus* (Mueller, 1938) Price, 1968 (see Margolis and Arthur, 1979) (Fig. 18:0)

Morphometric data (from Hanek and Fernando 1972a): body 540–924 long by 96–120 wide; dorsal hamuli 27–31 long, dorsal bar 27–31 transverse length; ventral hamuli 38–41 long, ventral bar 36–40 transverse length; marginal hooks 13–18 long; penis 43–46 long, accessory piece 38–42 long.

On gills, body surface and fins of *Ambloplites rupestris*
Records: Dechtiar 1972b (Ont); Hanek and Fernando 1972a (Ont); 1973b (Ont); 1974 (Ont); Molnar et al. 1974 (Ont); Hanek 1977 (Ont); Hanek and Fernando 1978a (Ont); 1978c (Ont); 1978e (Ont)
Remarks: This species was originally assigned to *Cleidodiscus* by Mueller (1938) and transferred to *Urocleidus* by Price (1967b). Following the emendation of the diagnoses of both genera by Beverley-Burton and Suriano (1980a) and Suriano and Beverley-Burton (1981), respectively, it is clear that *U. alatus* cannot be accommodated in either genus. Thus, further studies on living material are required before a generic designation is feasible.

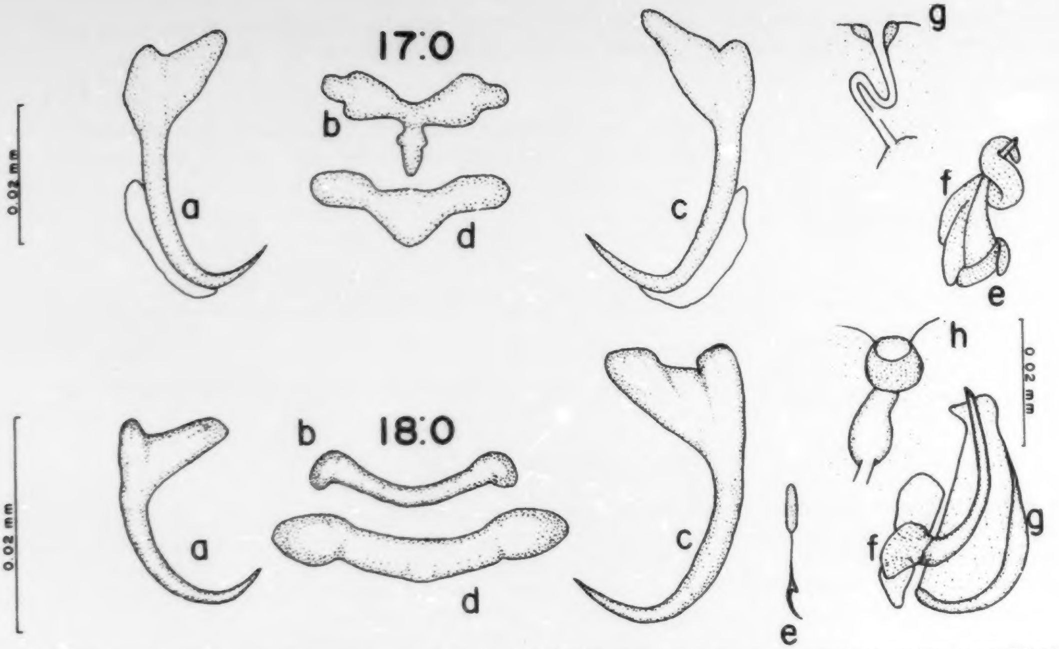


FIG. 17:0–18:0. Ancyrocephalid spp. of uncertain generic affinity. 17:0. "*Cleidodiscus*" *vancleavei* — *incertae sedis* (redrawn from Mizelle 1936): a. dorsal hamulus; b. dorsal bar; c. ventral hamulus; d. ventral bar; e. penis; f. accessory piece; g. vagina. 18:0. "*Urocleidus*" *alatus* — *incertae sedis* (redrawn from Mueller 1938): a. dorsal hamulus; b. dorsal bar; c. ventral hamulus; d. ventral bar; e. marginal hook; f. penis; g. accessory piece; h. vagina.

CAPSALIDAE Baird, 1853

Dactylogyrida: body flat, oval, often large; anterior extremity with pair of disc-like or sessile adhesive organs. Two pairs of eyes. Haptor disc-like and muscular, septate or nonseptate, typically with 14 marginal hooks; two pairs of hamuli and one pair of accessory sclerites (derived from marginal hooks of pair I) usually present; peripheral marginal hooks (pairs II–VII) present or absent. Mouth ventral, oral sucker lacking but pharynx well developed; caeca more or less branched, confluent posteriorly or not. Testes two or numerous; male and female pores separate, or close, or opening into genital atrium — submedian, lateral or marginal. Ovary median, usually pretesticular. Vagina present or absent (never double). Vitellaria extensive. Marine (rarely brackish water), typically (but not exclusively) on teleosts.

Key to genera of Capsalidae

1 More than two testes present (Fig. 20:0) 2

Two testes present (Fig. 19:0) 4

2 Haptor aseptate, forming an undivided disc (Fig. 22:0); anterior adhesive areas in form of two shallow grooves. On gills of sturgeons (*Acipenser* spp.) .... *Nitzschia*

Haptor septate, divided into loculi (Fig. 23:0); anterior adhesive areas disc- or sucker-like. Not on sturgeons 3

3 Anterior adhesive areas disc-like (Fig. 23:0); testicular follicles confined to intercaecal region; marginal spines of body large, pointed, bifid or serrate .... *Tristoma*

Anterior adhesive areas sucker-like (Fig. 20:0); testicular follicles extend lateral to caeca; marginal spines of body small, numerous, mostly quadricuspate, not bifid or serrate .... *Capsala*

4 **Haptor septate with central loculus and a variable number (6 in Canadian species) of peripheral loculi (Fig. 24:0); two pairs of hamuli, one pair of accessory sclerites. Anterior adhesive areas disc-like .... *Trochopus***

Haptor aseptate (Fig. 19:0) 5

5 **Anterior adhesive areas disc-like (Fig. 19:0). Haptor with two pairs of hamuli and one pair of accessory sclerites .... *Benedenia***

Anterior adhesive areas sessile and glandular (Fig. 21:0). Haptor with two pairs of hamuli and one pair of accessory sclerites .... *Entobdella*

Benedenia Diesing, 1858 (Fig. 19:0)

Capsalidae: anterior adhesive areas disc-like. Haptor aseptate with two pairs of hamuli and one pair of accessory sclerites, located anterior to hamuli. Pharynx lacking constriction or slightly constricted; caeca diverticulate, not confluent posteriorly. Testes two, in juxtaposition; genital pore on or near left body margin at varying levels behind left anterior adhesive disc. Ovary entire, median; vaginal opening submedian or near body margin. On gills of marine Perciformes. One species on Canadian fishes.

Benedenia derzhavini (Layman, 1930) Meserve, 1938

Morphometric data in Table 11.

On gills of *Sebastes crameri*; *S. proriger*; *S. reedi*; *S. variegatus*; *S. zacentrus*
Record: Sekerak and Arai 1977 (Pac)

TABLE 11. Comparative measurements (in mm) of *Benedenia derzhavini* (Layman, 1930) and *Entobdella* Blainville in Lamarck, 1818 spp. recorded from fishes of Canada.

Species	*B. derzhavini*	*E. curvunca*	*E. hippoglossi*	*E. pugetensis*
Source of data	Layman (1930)	Ronald (1957)	Price (1939)	Robinson (1961)
Body: length	6.0	7.0–13.0	13.03–18.0[a]	1.90–4.34
width	3.5	3.0–6.0	3.6–4.8[a]	0.72–2.32
Haptor: width	3.11	1.5–2.5	3.6–4.8	0.50–1.65
Accessory sclerites: length	0.30	0.39–0.46	0.51–0.64	0.12–0.31
Anterior hamuli: length	0.21	0.54–0.99	0.82–0.94	0.18–0.51
Posterior hamuli: length	0.20	0.09–0.12	0.10–0.12	0.10–0.17
Marginal hooks: total length	—	"approx." 0.06	"about" 0.02	—
Site	gills	body surface	body surface	body surface
Host(s)	*Sebastes crameri* *S. proriger* *S. reedi* *S. variegatus* *S. zacentrus*	*Hippoglossus hippoglossus*	*Hippoglossus hippoglossus* *H. stenolepis*	*Atheresthes stomias*
Locality(ies)	Pacific	Atlantic	Atlantic Pacific	Pacific

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[a] Ronald (1957) gave the size of *E. hippoglossi* as 13.0–24.0 mm long by 3.6–11.0 mm wide.

19:0

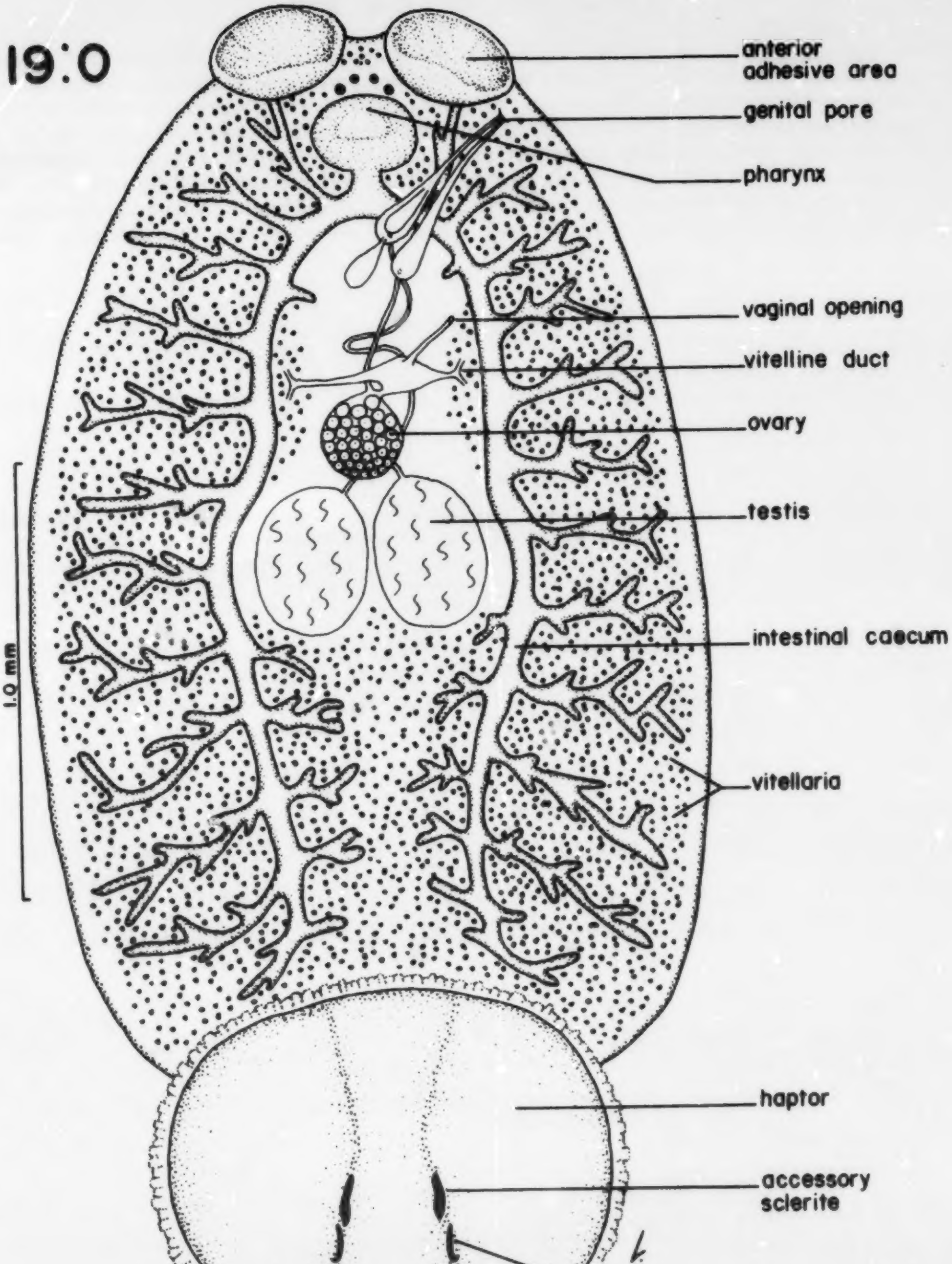
anterior adhesive area
genital pore
pharynx
vaginal opening
vitelline duct
ovary
testis
intestinal caecum
vitellaria
haptor
accessory sclerite
hamuli
1.0 mm

FIG. 19:0. *Benedenia* — generic characters (based on Bykhovsky 1957): whole animal, ventral view.

Capsala Bosc, 1811 (Fig. 20:0)

Capsalidae: anterior adhesive areas sucker-like. Body with conspicuous median notch posteriorly; dorsal and lateral spines present on body margins. Haptor septate, with polygonal, central loculus and seven peripheral loculi, posterior septa not bifid distally; hamuli lacking; one pair of accessory sclerites (derived from marginal hooks pair I) present or not[36] and 12 marginal hooks. Pharynx with median constriction; caeca diverticulate, confluent posteriorly. Testes follicular, numerous, extending laterally beyond caeca; genital pore submarginal, left, near left adhesive area. Ovary lobed, median; vitellaria with numerous follicles extending towards all body margins but absent from region of anterior adhesive areas and haptor. Vaginal opening on left, in intercaecal area, posterior to genital pore. On body surface of marine teleosts. One species on Canadian fishes.

Capsala martinierei Bosc, 1811

Morphometric data in Table 12.

On body surface of *Mola mola*

Records: de La Martinière 1787 (Pac); 1797 (Pac); Stafford 1904 (Atl); 1907 (Atl); Threlfall 1967 (Atl); Logan and Odense 1974 (Atl)

Remarks: Margolis and Arthur (1979) provided a brief synopsis of the early history concerning the naming of *C. martinierei*.

TABLE 12. Comparative measurements (in mm, except where otherwise noted) of *Capsala martinierei* Bosc, 1811, *Nitzschia sturionis* (Abildgaard 1794), *Tristoma* Cuvier, 1817 spp. and *Trochopus* Diesing, 1850 spp. recorded from fishes of Canada.

Species	*Capsala martinierei*	*Nitzschia sturionis*	*Tristoma coccineum*	*Tristoma integrum*	*Trochopus marginata*	*Trochopus trituba*
Source of data	Price (1939)	Price (1939)	Price (1939)	Price (1939)	Folda (1928)	Pratt and Aldrich (1953)
Body: length	15.0–21.0	8.0–15.0	10.0–12.0^{b}	0.58–7.0^{b}	1.92–4.43	6.7–9.5
width	16.0–21.0	2.1–3.5	7.0–9.5	6.0–6.5	0.58–1.23	3.3
Haptor: width	8.0–10.0	—	1.8–2.38	1.4–1.6	0.58–1.24^{c}	2.75^{c}
Accessory sclerites: length	lacking	85–120^{a}	133–152^{a,d}	110–133^{a,d}	70–150^{a}	155^{a}
Anterior hamuli: length	lacking	106–167^{a}	—	—	90–140^{a}	110^{a}
Posterior hamuli: length	lacking	106–167^{a}	—	—	110–140^{a}	130^{a}
Marginal spines (rows)	none present	none present	43–54	up to "more than 300"	none present	none present
Spines per row	—	—	2–4	6 usually	—	—
Site(s)	body surface	gills	gills and gill cavity	gills	gills	gills
Host(s)	*Mola mola*	*Acipenser oxyrhynchus*	*Xiphias gladius*	*Xiphias gladius*	*Sebastes alutus* *S. caurinus* *S. maliger* *S. nebulosus*	*Sebastes caurinus* *S. pinniger*
Locality(ies)	Atlantic Pacific	Atlantic New Brunswick	Atlantic	Atlantic	Pacific	Pacific

[a] Micrometres (μm).

[b] Maxima provided by Iles (1971) (for specimens frozen before fixation) were 16.37 for *T. coccineum* and 12.00 for *T. integrum* Iles (1971) also discussed the relationship between body length and numbers of rows of spines in immature and mature specimens.

[c] Including membrane.

[d] See generic diagnosis for *Tristoma*.

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[36] Price (1939) noted that "hooks" (= accessory sclerites) are absent in *C. martinierei* and this is confirmed by the present author having examined material from *Mola mola* taken off New Brunswick.

20:0

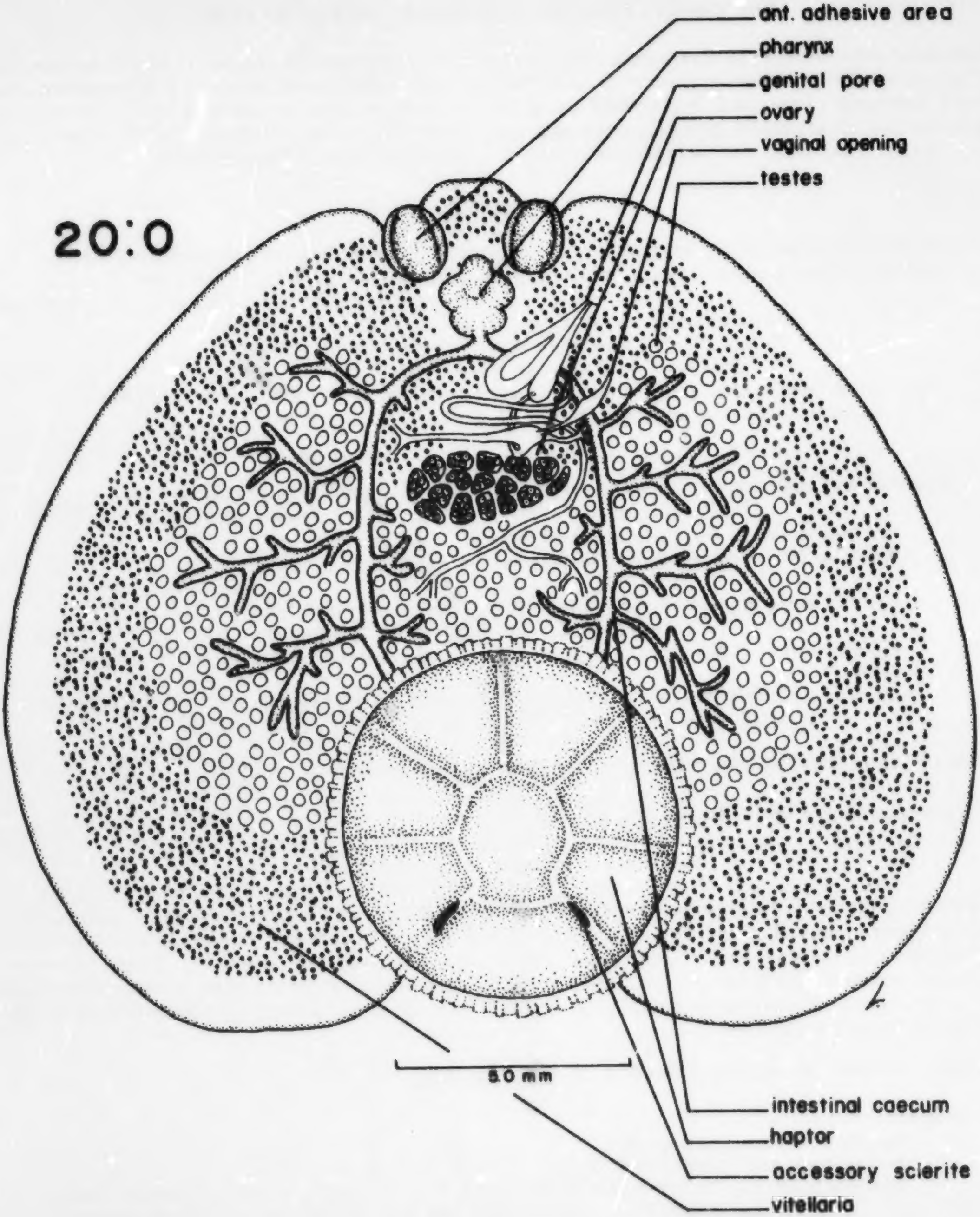
ant. adhesive area
pharynx
genital pore
ovary
vaginal opening
testes
5.0 mm
intestinal caecum
haptor
accessory sclerite
vitellaria

FIG. 20:0. *Capsala* — generic characters (based on Price 1939 with original observations): whole animal, ventral view.

Entobdella Blainville in Lamarck, 1818 (Fig. 21:0)

Capsalidae: anterior adhesive areas sessile, not disc-like. Haptor aseptate with two pairs of hamuli and one pair of accessory sclerites located anterior to hamuli. Pharynx with median constriction; caeca diverticulate, confluent posteriorly. Testes two, in juxtaposition; genital pore on left body margin near base of left anterior adhesive area. Ovary entire, median, pretesticular; vagina opening on left in intercaecal area behind genital pore; vitellaria extensive. On body surface of marine teleosts and (rarely) elasmobranchs.

Key to species of *Entobdella*

1 Haptoral papillae absent; anterior adhesive areas with muscular components producing triloculate appearance. Body not more than 5 mm long. Not parasitic on *Hippoglossus* spp. .... *E. pugetensis* Robinson, 1961 (Fig. 21:3, Table 11)

On body surface of *Atheresthes stomias*
Record: McDonald 1981 (pers. comm.) (Pac) — new Canadian host record[37]

Haptoral papillae present; anterior adhesive areas not divided. Body robust, more than 5 mm long. On *Hippoglossus* spp. (Atlantic and Pacific) 2

2 Anterior and posterior hamuli with curved root; body 7–13 mm long .... *E. curvunca* Ronald, 1957 (Fig. 21:1, Table 11)

On body surface of *Hippoglossus hippoglossus*
Records: Ronald 1957 (Atl); 1960 (Atl)

Anterior and posterior hamuli with straight root; body 13–24 mm[38] long .... *E. hippoglossi* (Mueller, 1776) Johnston, 1856 (Fig. 21:2, Table 11)

On body surface of *Hippoglossus hippoglossus* (1,2,3,4,5); *H. stenolepis* (6); *Reinhardtius hippoglossoides* (7)
Records: 1. Stafford 1904 (Atl); 2. 1907 (Atl); 3. Cooper 1921 (Atl); 4. Ronald 1957 (Atl); 5. 1960 (Atl); 6. Hoskins et al. 1976 (Pac); 7. Redkozubova 1976 (Atl)

Record of an unidentified *Entobdella* sp. listed from the following:

Pleuronectidae gen. sp. — Hoskins et al. 1976, Pacific.

Nitzschia von Baer, 1826 (Fig. 22:0)

Capsalidae: anterior adhesive areas shallow, weakly muscular grooves into which cephalic glands open. Haptor aseptate, muscular, with two pairs of hamuli and one pair of accessory sclerites located anterior to hamuli. Pharynx lacking constriction; caeca diverticulate, not confluent posteriorly. Testes numerous, median, confined to intercaecal area; genital pore submedian, postbifurcal. Ovary entire, pretesticular; vagina with median opening, posterior to genital pore. Brackish water, on gills of sturgeons (Acipenseriformes). One species on Canadian fishes.

Nitzschia sturionis (Abildgaard, 1794) Krøyer, 1852 (Fig. 22:1)

Morphometric data in Table 12.

On gills of *Acipenser oxyrhynchus*
Record: Appy and Dadswell 1978 (NB-b)
Remarks: Bykhovsky (1957) named *N. superba* MacCallum, 1921 as a synonym of *N. sturionis*, which is the type species. Price (1939) cited a record of *N. sturionis* (named as *N. elegans*) from *A. sturio* as being from Stafford (1904), which is incorrect.

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[37] Additional Canadian record: Arthur (1984. Can. J. Zool. 62: 675–684), from *Theragra chalcogramma* — Pacific. Arthur considered this record as likely the result of "interhost transfer during host capture".

[38] From Ronald (1957).

21:0

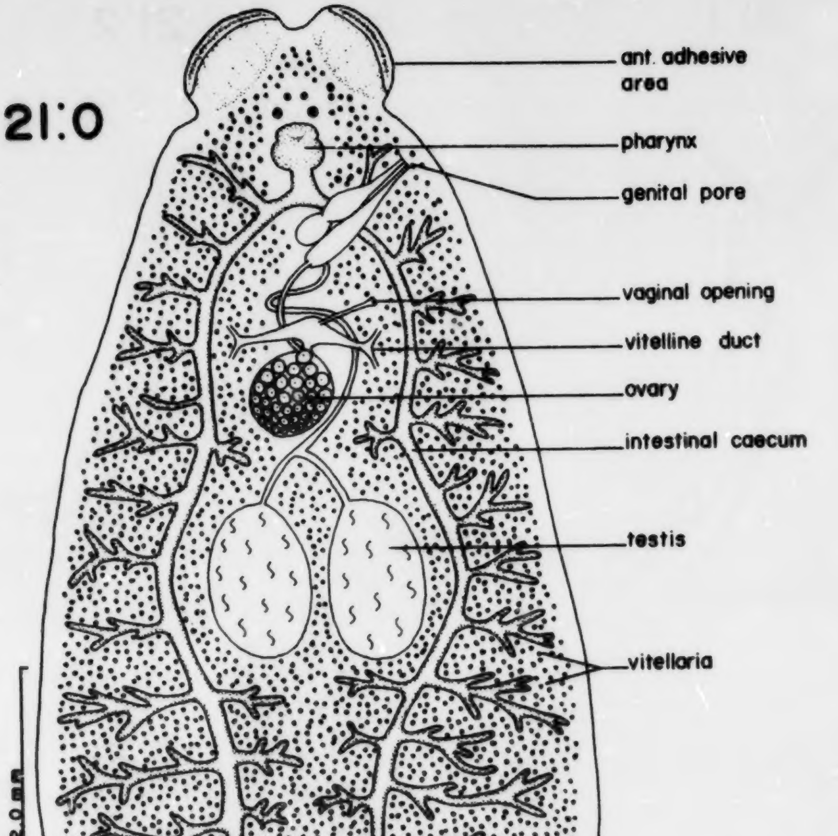
ant. adhesive area
pharynx
genital pore
vaginal opening
vitelline duct
ovary
intestinal caecum
testis
vitellaria
2.0 mm
haptor
accessory sclerite
hamuli
L

FIG. 21:0. *Entobdella* — generic characters (original): whole animal, ventral view.

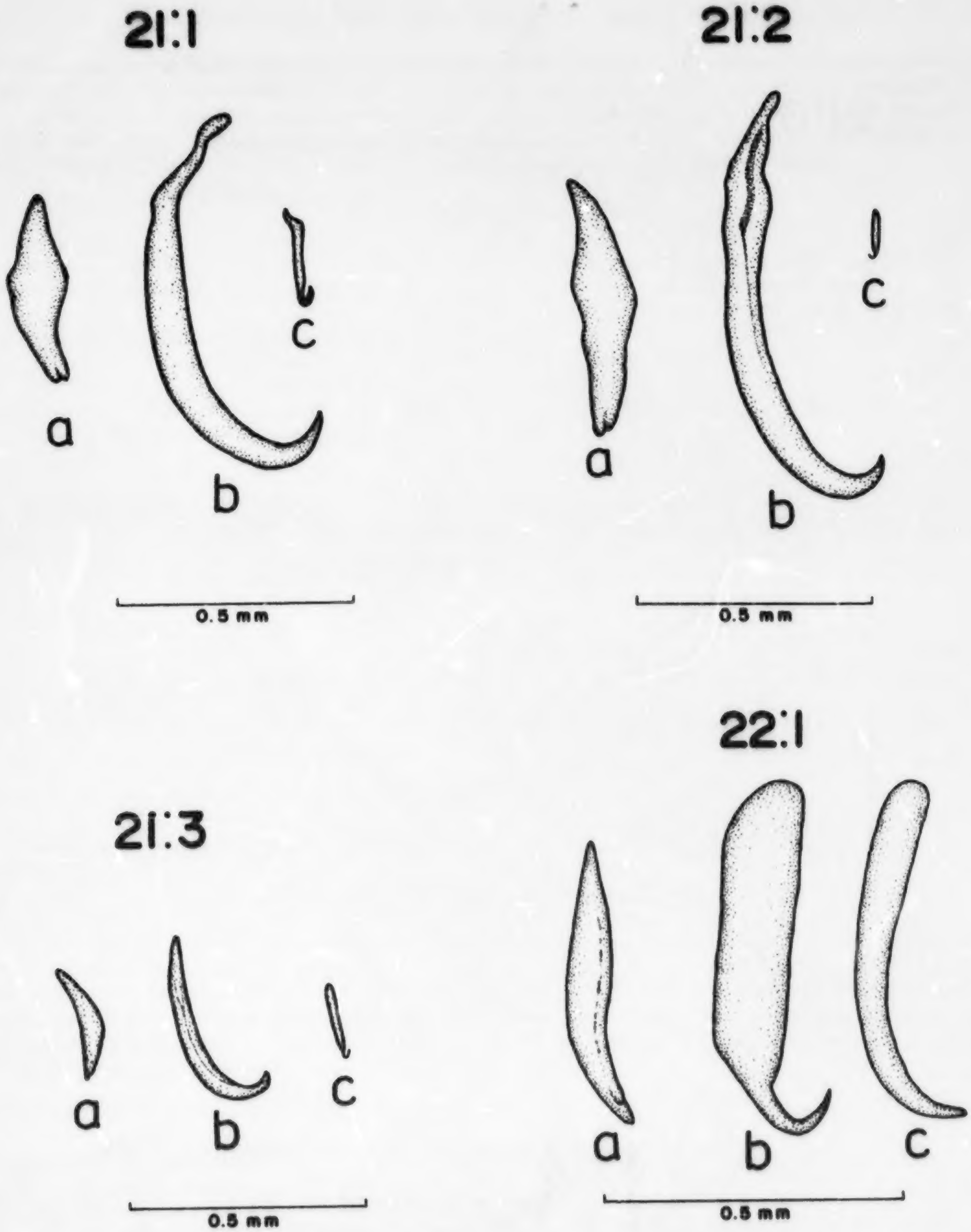

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FIG. 21:1–21:3 and 22:1. *Entobdella* spp. and *Nitzschia sturionis*. 21:1. *E. curvunca* (modified from Ronald 1957): a. accessory sclerite; b. anterior hamulus; c. posterior hamulus. 21:2. *E. hippoglossi* (modified from Price 1939): a. accessory sclerite; b. anterior hamulus; c. posterior hamulus. 21:3. *E. pugetensis* (modified from Robinson 1961): a. accessory sclerite; b. anterior hamulus; c. posterior hamulus. 22:1. *N. sturionis* (modified from Price 1939): a. accessory sclerite; b. anterior hamulus; c. posterior hamulus.

22:0

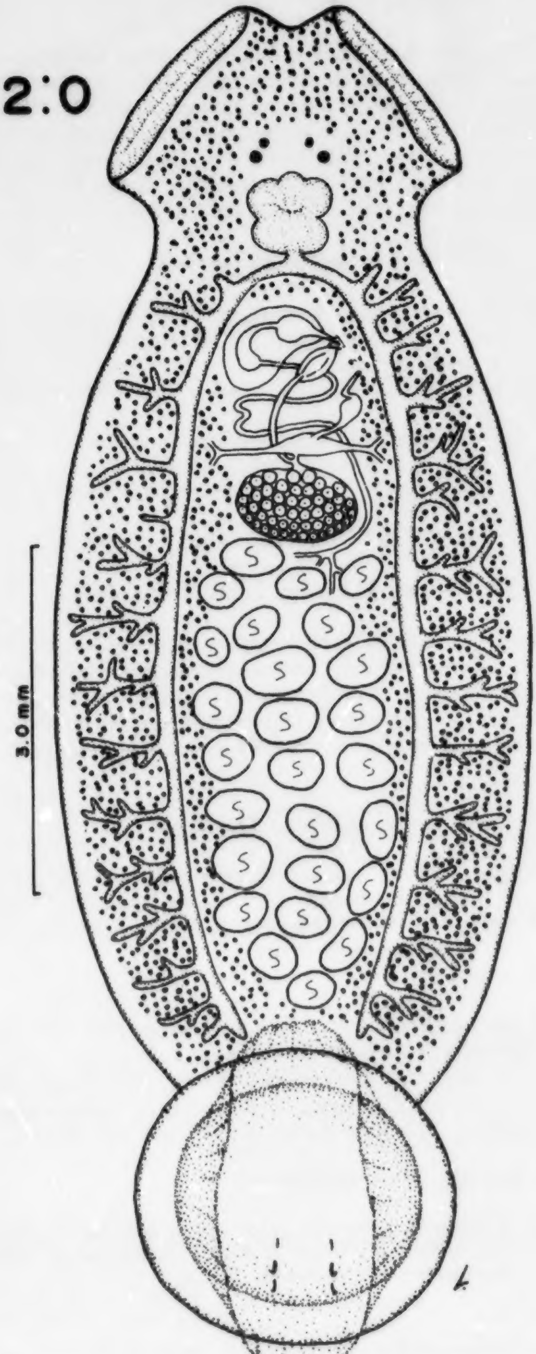

FIG. 22:0. *Nitzschia* — generic characters (original): whole animal, ventral view.

Tristoma Cuvier, 1817 (Fig. 23:0)

Capsalidae: anterior adhesive areas disc-like. Body with slight median notch posteriorly; spines present on lateral margins and dorsal surface in numerous, transverse rows. Haptor septate with polygonal central loculus and seven loculi; posterior septa not bifid distally; one pair of "hamuli".[39] Pharynx lacking constriction; caeca diverticulate, confluent posteriorly. Testes follicular, numerous, confined to median area bounded by caeca; genital pore submarginal, posterior to left adhesive disc. Ovary lobed, median; vitellaria with numerous follicles extending to lateral and posterior body margins but absent from anterior adhesive discs and haptor; vagina on left, posterior to genital pore. On gills (and in gill cavity) of marine teleosts.

Key to species of *Tristoma*

1 Body length up to 16.4 mm;[40] dorsomarginal rows of spines 43–54 in number with 2–4 differently shaped spines per row. Of common occurrence ... *T. coccineum* Cuvier, 1817 (Fig. 23:1, Table 12)

On gills and gill cavity of *Xiphias gladius*
Records: Stafford 1904 (Atl); 1907 (Atl); Iles 1971 (Atl); Uhazy 1980 (pers. comm.) (Atl)

Body length up to 12.0 mm;[40] dorsomarginal rows of spines greater than 300 in number with (usually) 6 similarly shaped spines per row. Of comparatively rare occurrence .... *T. integrum* Diesing, 1850 (Fig. 23:2, Table 12)

On gills of *Xiphias gladius.*
Records: Iles 1971 (Atl); Uhazy 1980 (pers. comm.) (Atl)

Trochopus Diesing, 1850 (Fig. 24:0)

Capsalidae: anterior adhesive areas disc-like. Haptor septate, divided by a variable number of radial septa (5–10[41]) into central loculus, which is open posteriorly, and peripheral loculi; two pairs of hamuli and one pair of accessory sclerites, lying anterior to hamuli. Pharynx lacking constriction; caeca diverticulate, not confluent posteriorly. Testes two, in juxtaposition; genital pore near left body margin immediately posterior to adhesive disc. Ovary entire, median, pretesticular; vaginal opening alongside genital pore; vitellaria extensive. On gills of marine teleosts.

Key to species of *Trochopus*

1 Body length greater than 6 mm; central loculus of haptor with wide anterior region (wider than length of anchors); posterior hamuli D-shaped .... *T. trituba* (Pratt and Aldrich, 1953) Bravo-Hollis, 1958 (Fig. 24:2, Table 12)

On gills of *Sebastes caurinus, S. pinniger*
Record: Hoskins et al. 1976 (Pac)

Body length less than 4.5 mm; central loculus of haptor with narrow anterior region (not wider than length of anchors); posterior hamuli not D-shaped .... *T. marginata* (Folda, 1928) Price, 1936 (Fig. 24:1, Table 12)

On gills of *Sebastes alutus* (2,3); *S. caurinus* (1,3); *S. maliger* (3); *S. nebulosus* (3)
Records: 1. Arai 1969 (Pac); 2. Sekerak and Arai 1973 (Pac); 3. 1977 (Pac)

Records of unidentified *Trochopus* spp. are listed from:

Sebastes aleutianus, S. alutus, S. babcocki, S. borealis, S. brevispinis, S. crameri, S. diploproa, S. elongatus, S. entomelas, S. flavidus, S. goodei, S. pinniger, S. proriger, S. reedi, S. ruberrimus, S. zacentrus — Sekerak and Arai 1977, Pacific; *S. zacentrus* — Hoskins et al. 1976, Pacific.

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[39] It is not known if these sclerotized components are hamuli or accessory sclerites derived from a pair of centrally placed marginal hooks.

[40] See Table 12.

[41] See Arai and Koski (1964).

23:0

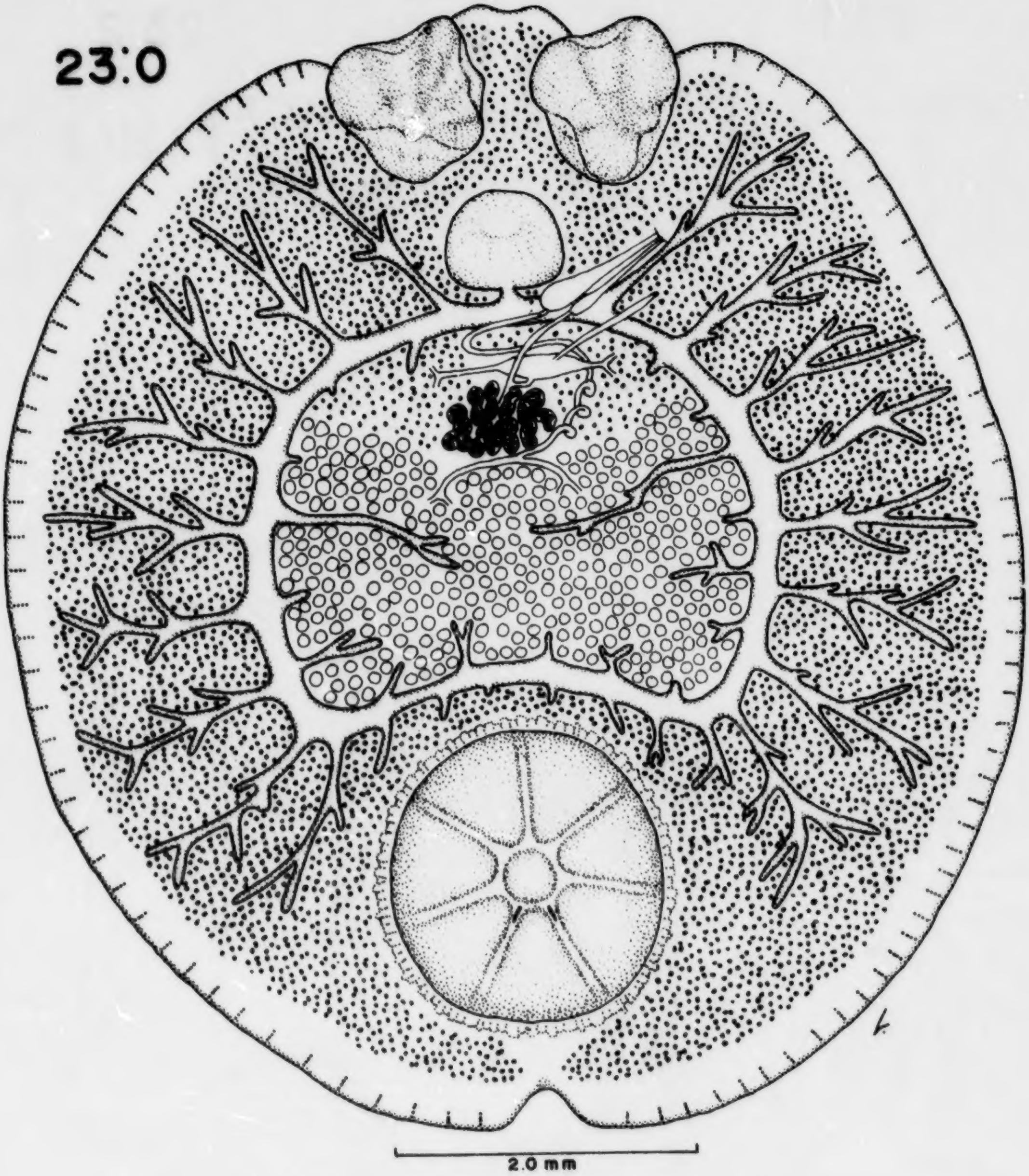

FIG. 23:0. *Tristoma* — generic characters (original): whole animal, ventral view.

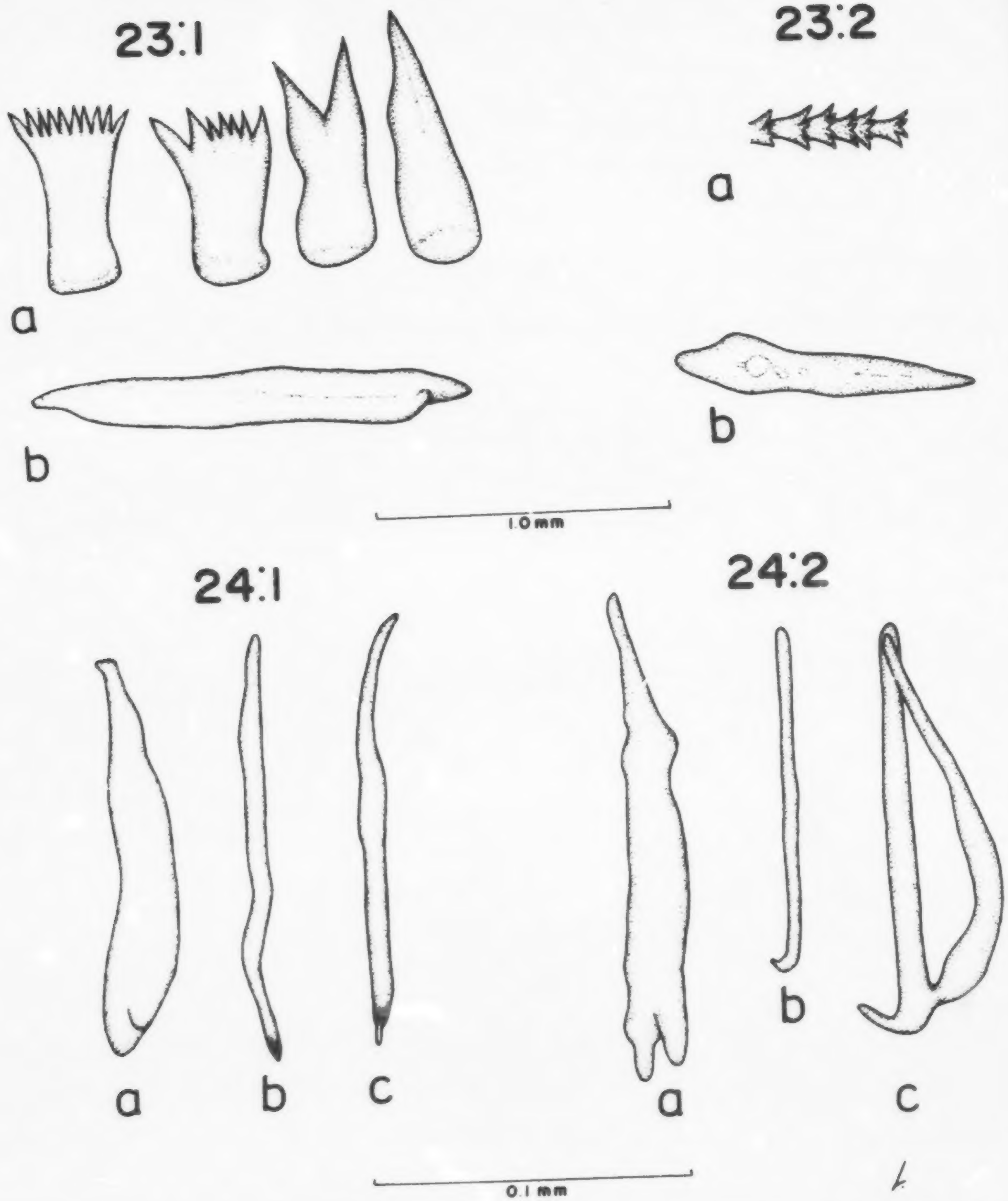

FIG 23:1–23:2 and 24:1–24:2. *Tristoma* spp. and *Trochopus* spp. 23:1. *Tristoma coccineum* (redrawn from Price 1939): a. dorsal marginal spines; b. "hamulus" — see text. 23:2. *Tristoma integrum* (redrawn from Price 1939): a. dorsal marginal spines; b. "hamulus" — see text. 24:1. *Trochopus marginata* (redrawn from Price 1939): a. accessory sclerite; b. anterior hamulus; c. posterior hamulus. 24:2. *Trochopus trituba* (redrawn from Pratt and Aldrich 1953): a. accessory sclerite; b. anterior hamulus; c. posterior hamulus.

24:0

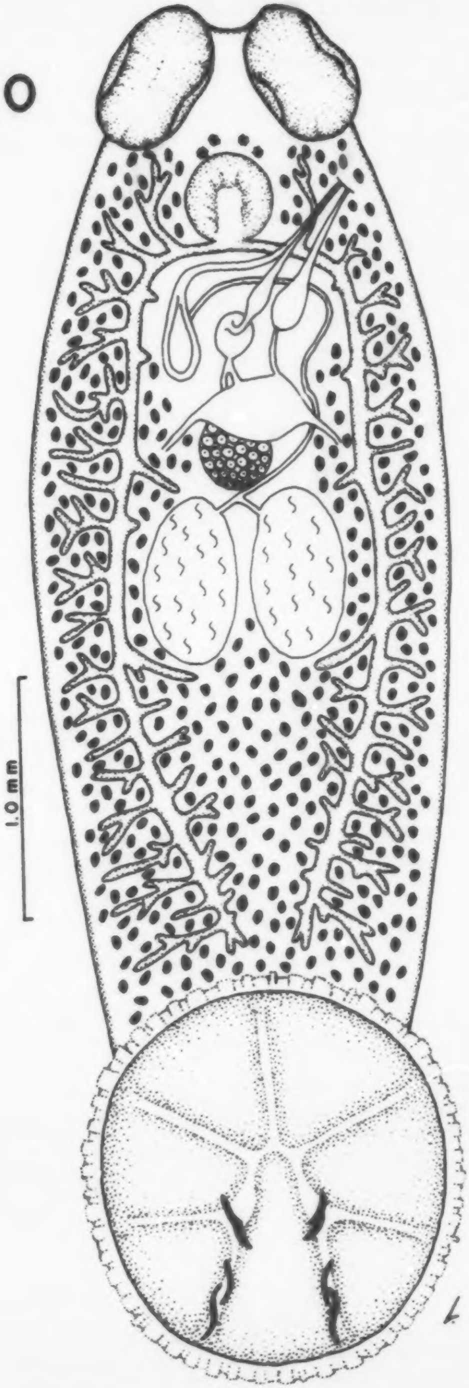

FIG. 24:0. *Trochopus* — generic characters (based on Folda 1928): whole animal, ventral view.

DACTYLOGYRIDAE Bykhovsky, 1933

Dactylogyrida: body small, anterior extremity with cephalic lobes; head organs present; cephalic glands in two groups in anterolateral region of body. Two pairs of eyes. Haptor more or less distinct with 14 marginal hooks of which 12 are peripheral and two central; hamuli and bar(s) present or, secondarily, absent. If present, dorsal hamuli conspicuous, associated with dorsal transverse bar, ventral hamuli and bar vestigial (or lacking). Mouth ventral, pharynx present, intestinal caeca confluent posteriorly. Testis single, intercaecal, postovarian; vas deferens (where observed) looping dorsoventrally round left intestinal caecum, expanding to form seminal vesicle; penis sclerotized tube with variable accessory piece. Ovary narrowing towards ootype without looping round intestine; vaginal pore single. Freshwater, typically (but not exclusively) on Cypriniformes.

Key to genera of Dactylogyridae

1 Hamuli and bar(s) lacking (Fig. 25:0 and 28:0) 2

Hamuli and bar(s) present (Fig. 26:0 and 27:0) 3

2 Haptor poorly developed (Fig. 25:0). Cuticle markedly thickened. Adult worms lacking defined eye spots (although scattered pigment granules may persist). In ureters of Cypriniformes or, more rarely, centrarchids .... *Acolpenteron*

Haptor well developed (Fig. 28:0). Cuticle not thickened. Adult worms with discrete eye spots. On gills and fins of cyprinids .... *Pseudacolpenteron*

3 Deep root of dorsal hamuli larger than superficial root, point may be doubly curved; ventral hamuli vestigial; dorsal transverse bar almost oval in shape, ventral bar lacking (Fig. 27:0). In nasal cavities (rarely gills)[42] of catostomids .... *Pellucidhaptor*

Deep root of dorsal hamuli not as large as superficial root; ventral hamuli vestigial;[43] transverse bar(s) usually bowed, dorsal bar often with lateral articulatory inflations, ventral bar vestigial or lacking (Fig. 26:0). On gills (rarely skin) of Cypriniformes (primarily) .... *Dactylogyrus*

Acolpenteron Fischthal and Allison, 1940 (Fig. 25:0)

Dactylogyridae: body elongate, cuticle thick. Head organs poorly defined. Eyespots represented by scattered pigment granules. Haptor spatulate with 14 marginal hooks; hamuli and bar(s) lacking. Penis sclerotized looping tube; accessory piece triradiate. Ovary oval, median. Vagina ventral, near right margin; seminal receptacle present. Vitellaria filling available space between pharynx and caecal confluence. In ureters and urinary bladder of North American (and Eurasian) freshwater fishes (Cypriniformes and, more rarely, Centrarchidae). One species in Canadian fishes.

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[42] Outside Canada *Pellucidhaptor* spp. have been found on body surface of their hosts.

[43] Kearn (1968) detailed the development of the haptoral sclerites of "*Neodactylogyrus*" *crucifer* (Wagener, 1857) and noted the presence of vestigial sclerites, which he considered to be reduced ventral hamuli. Similar patterns of development were observed in three other *Dactylogyrus* spp. and Kearn (1968) concluded that the extra pair of sclerites described by Mizelle and Price (1963) as an additional, eighth pair, of marginal hooks (4A) are vestigial ventral hamuli (see footnote 49).

25:0

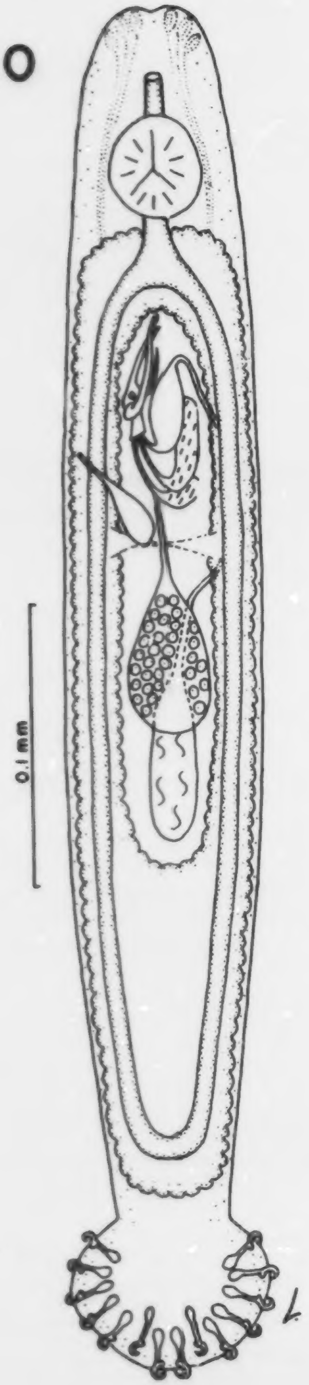

FIG. 25:0. *Acolpenteron* — generic characters (based on Fischthal and Allison 1941, 1942): whole animal, ventral view.

Acolpenteron catostomi Fischthal and Allison, 1942 (Fig. 25:1)

Morphometric data (from Fischthal and Allison 1942): body 480 × 90; haptor 61 wide; marginal hooks 30–32[44] long. Pharynx 41 diameter. Testis 64 by 15; ovary 71 by 27.

In ureters of *Carpiodes cyprinus* (1); *Catostomus catostomus* (3,4,8); *C. commersoni* (1,2,5,6,7); *C. macrocheilus* (4,8)

Records: 1. Dechtiar 1972b (Ont); 2. 1972c (Ont); 3. Hanek and Molnar 1974 (Que); 4. Anon. 1978 (BC); 5. Lubinsky and Loch 1979 (Man); 6. Cone 1980 (NB); 7. Murith 1983 (pers. comm.) (Ont); 8. Arai and Mudry 1983 (BC)

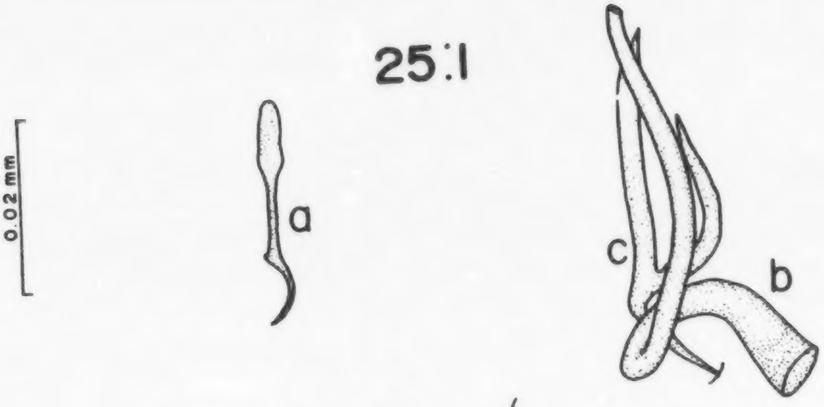

FIG 25:1. *Acolpenteron catostomi* (modified from Fischthal and Allison 1942): a. marginal hook; b. penis; c. accessory piece.

Dactylogyrus Diesing, 1850 (Fig. 26:0)

Dactylogyridae: body elongate. Head organs well defined. Haptor with one pair of conspicuous, dorsal hamuli associated with dorsal transverse bar; ventral hamuli and bar vestigial; 14 marginal hooks of similar shape (but size may be variable). Vas deferens (when observed) looping left intestinal caecum; penis tubular, variable in shape (e.g. straight, curved, coiled or whip-like); accessory piece variable. Vagina present, ventral, usually on right. Vitellaria coextensive with intestine and extending laterally to body margin. On gills of freshwater fishes (primarily Cypriniformes).

Remarks: Price (1938b), in an effort to split the genus *Dactylogyrus*, proposed *Neodactylogyrus* for species in which two haptoral bars were present. Mizelle and Donahue (1944) rejected *Neodactylogyrus* because of the difficulty of seeing the ventral (vestigial) bar in prepared mounts. Most authors have followed Mizelle and Donahue (1944) although the name *Neodactylogyrus* was retained by Sproston (1946), Yamaguti (1963), Kearn (1968), and Lambert (1977). Having reviewed the *Dactylogyrus* spp. from Canadian fishes, a taxonomic regrouping has not been attempted although the genus may eventually be split on the basis of characters associated with the male genitalia (penis types) rather than variations (e.g. presence/absence of the ventral bar) in the haptoral sclerites.

Key to species of *Dactylogyrus*

1 Parasites of cyprinids 5

Parasites of fishes other than cyprinids 2

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[44] From Murith 1983 (pers. comm.). Fischthal and Allison (1942) gave this measurement as 23.

26:0

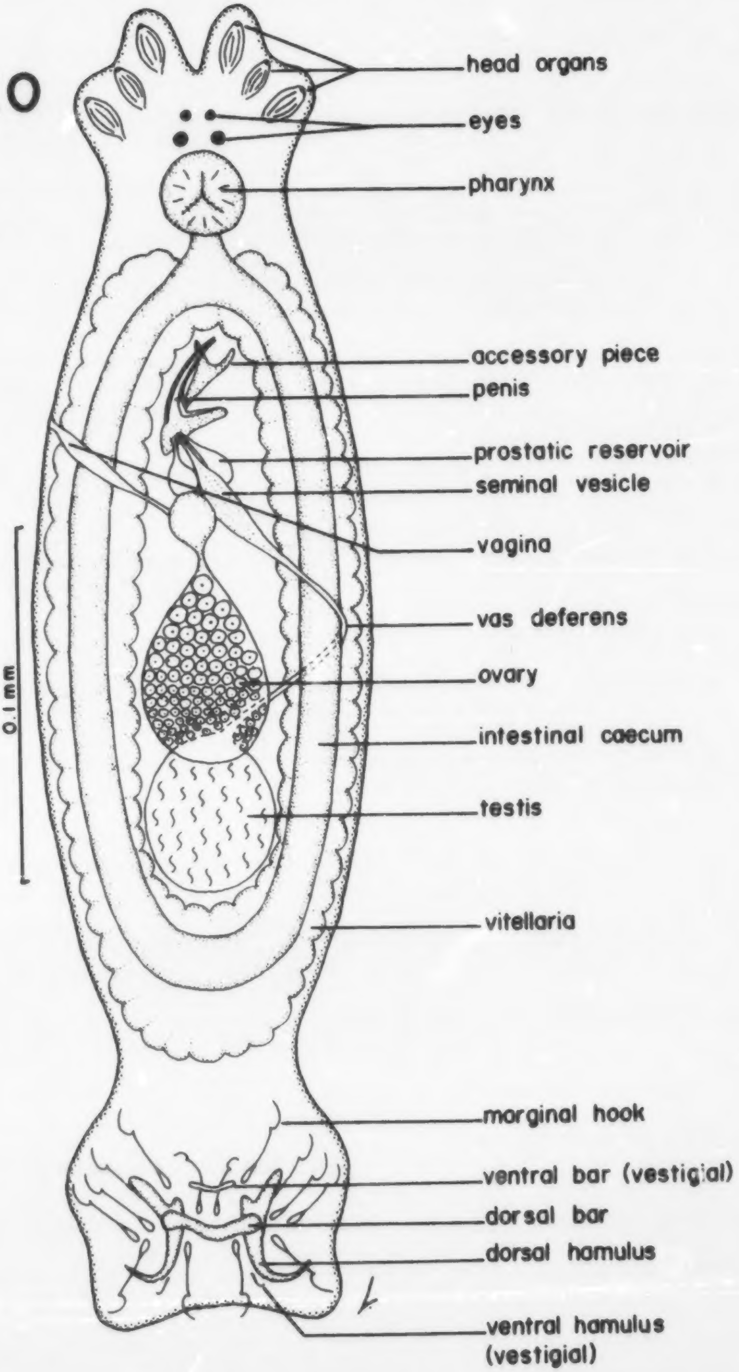
head organs
eyes
pharynx
accessory piece
penis
prostatic reservoir
seminal vesicle
vagina
vas deferens
ovary
intestinal caecum
testis
vitellaria
marginal hook
ventral bar (vestigial)
dorsal bar
dorsal hamulus
ventral hamulus (vestigial)
0.1 mm

FIG. 26:0. *Dactylogyrus* — generic characters (original): whole animal, ventral view.

2 Parasites of catostomids 3

Parasites of cottids or gasterosteids 4

3 Penis elongate, with slightly expanded base; accessory piece triradiate, distal limb with exterior projection .... *D. urus* Mueller, 1938 (Fig. 26:37, Table 18)

On gills of *Moxostoma anisurum* (1); *M. erythrurum* (2,3)
Records: 1. Dechtiar 1972b (Ont); 2. 1972c (Ont); 3. Lubinsky and Loch 1979 (Man)
Remarks: *D. urus* and *D. apos* (both proposed by Mueller 1938) are the only two *Dactylogyrus* spp. recorded from catostomids in Canada and are, in many respects, similar. In the present key these species are separated on depicted differences in the male copulatory complexes which appear to have been distorted by coverslip pressure. It is suggested that, following examination of fresh material, they may prove synonymous.

Penis "robust",[45] with proximally inflated base, distal region reflected at an obtuse angle from base; accessory piece triradiate, distal limb with bifid tip .... *D. apos* Mueller, 1938 (Fig. 26:3, Table 18)

On gills of *Hypentelium nigricans*
Record: Hanek et al. 1975 (Ont)
Remarks: See *D. urus* above.

4 On *Cottus* spp. Penis curving, tubular, with distinctly flared base; accessory piece triradiate .... *D. buddi* Dechtiar, 1974 (Fig. 26:9, Table 18)

On gills of *Cottus bairdi* (1); *C. cognatus* (1,2)
Records: 1. Dechtiar 1974b (Ont); 2. Arthur et al. 1976 (YT)

On *Culaea inconstans*. Penis almost straight, tubular, with slightly flared base; accessory piece triradiate .... *D. eucalius* Mizelle and Regensberger, 1945 (Fig. 26:20, Table 18)

On gills of *Culaea inconstans*
Records: Dechtiar 1972b (Ont); Hanek and Fernando 1972b (Ont); Hanek et al. 1975 (Ont): Lubinsky and Loch 1979 (Man)

5 Penis tubular, usually short, straight or only slightly curved; accessory piece basically triradiate (with distal component guiding distal part of penis) 13

Penis tubular, elongate, straight, curved, coiled or whip-like; accessory piece not triradiate 6

6 Penis tubular, forming spiral (with 4 coils) .... *D. eos* Hanek, Molnar and Fernando, 1975 (Fig. 26:19, Table 13)

On gills of *Chrosomus eos*
Records: Hanek et al. 1975 (Ont); Cone 1980 (NB)

Penis tubular, but not forming spiral 7

7 Penis elongate and whip-like; accessory piece complex, forming grooved guide distally 8

Penis not elongate and whip-like; accessory piece not forming grooved guide distally 9

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[45] As described by Mueller (1938): no indication of length was provided.

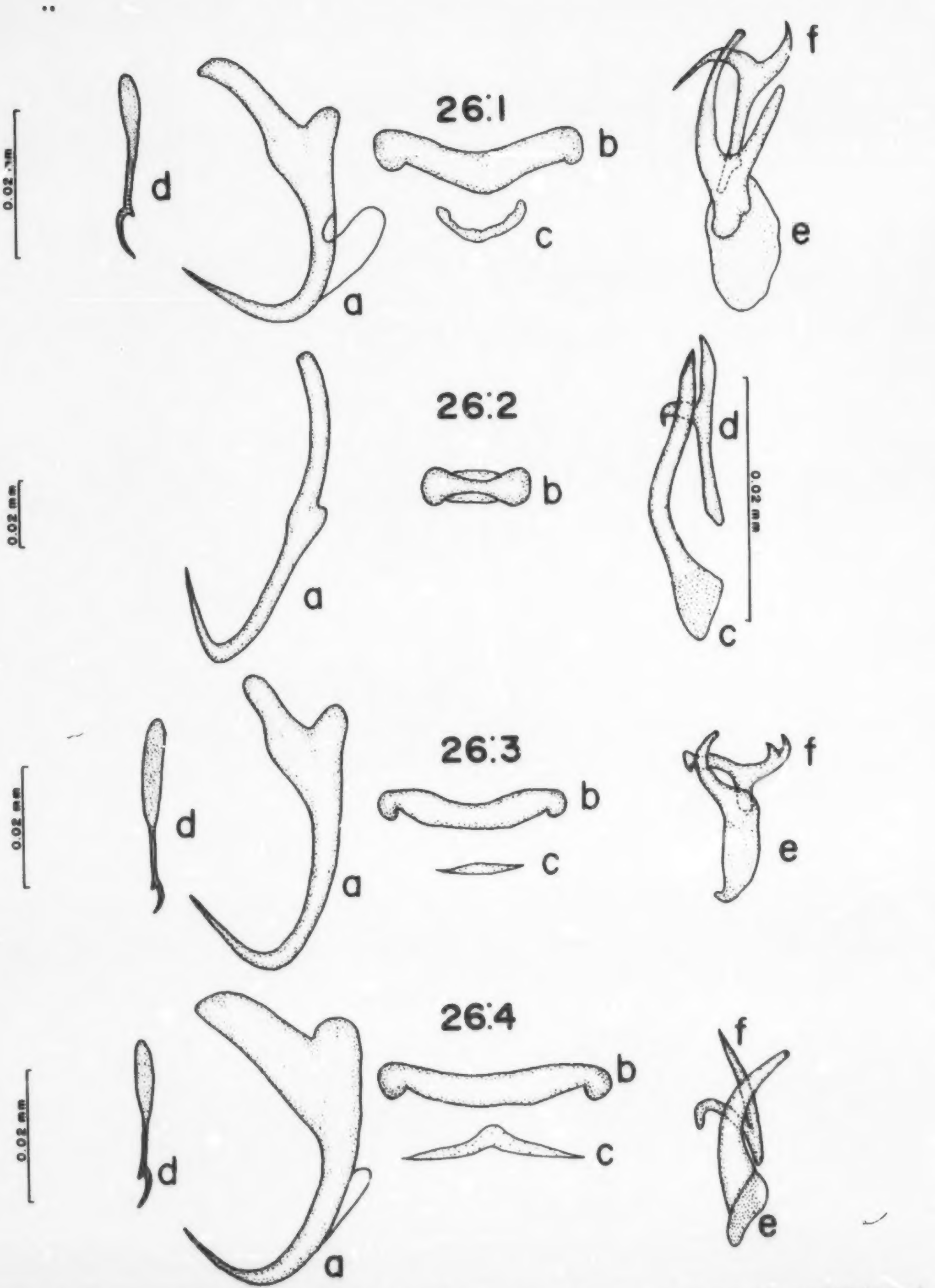

26:1
0.02 mm
a
b
c
d
e
f
26:2
0.02 mm
a
b
c
d
0.02 mm
26:3
0.02 mm
a
b
c
d
e
f
26:4
0.02 mm
a
b
c
d
e
f

FIG. 26:1–26:4. *Dactylogyrus* spp. 26:1. *D. albertensis* (modified from Price and Arai 1967): a. hamulus; b. dorsal bar; c. vestigial ventral bar; d. marginal hook; e. penis; f. accessory piece. 26:2. *D. anchoratus* (a, b modified from Bykhovsky 1957, c, d from Bykhovskaya-Pavlovskaya et al. 1962): a. hamulus; b. dorsal bar; c. penis; d. accessory piece. 26:3. *D. apos* (modified from Mueller 1938): a. hamulus; b. dorsal bar; c. vestigial ventral bar; d. marginal hook; e. penis; f. accessory piece. 26:4. *D. attenuatus* (modified from Mizelle and Klucka 1953): a. hamulus; b. dorsal bar; c. vestigial ventral bar; d. marginal hook; e. penis; f. accessory piece.

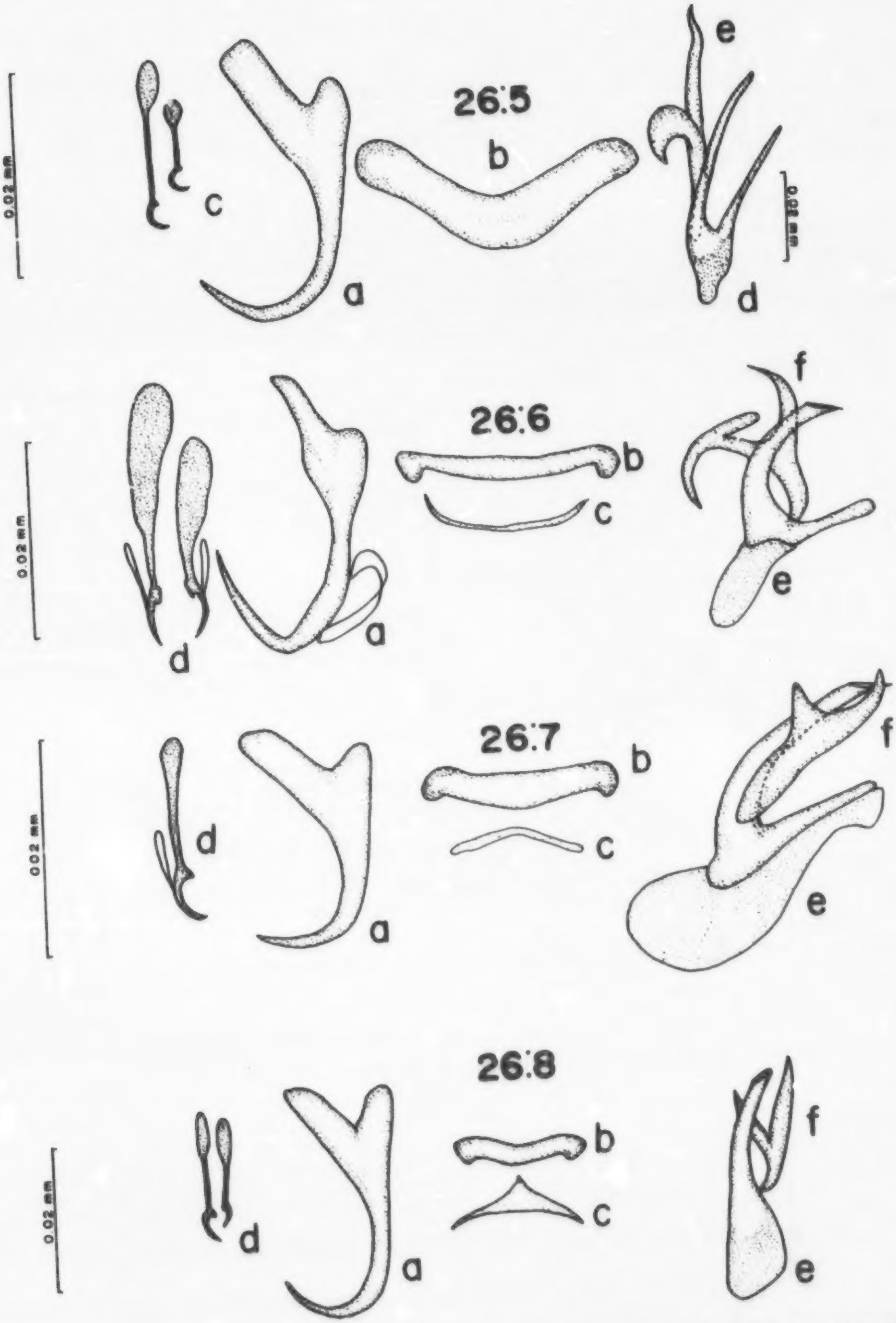

26:5
0.02 mm
c
a
b
e
d
0.02 mm
26:6
0.02 mm
d
a
b
c
f
e
26:7
0.02 mm
d
a
b
c
f
e
26:8
0.02 mm
d
a
b
c
f
e

FIG. 26:5–26:8. *Dactylogyrus* spp. 26:5. *D. aureus* (modified from Seamster 1948 and Hargis 1953): a. hamulus; b. dorsal bar; c. marginal hooks; d. penis; e. accessory piece. 26:6. *D. aviunguis* (modified from Chien 1974a): a. hamulus; b. dorsal bar; c. vestigial ventral bar; d. marginal hooks; e. penis; f. accessory piece. 26:7. *D. banghami* (modified from Monaco and Mizelle 1955): a. hamulus; b. dorsal bar; c. vestigial ventral bar; d. marginal hook; e. penis; f. accessory piece. 26:8. *D. bifurcatus* (modified from Mizelle 1938): a. hamulus; b. dorsal bar; c. vestigial ventral bar; d. marginal hooks; e. penis; f. accessory piece.

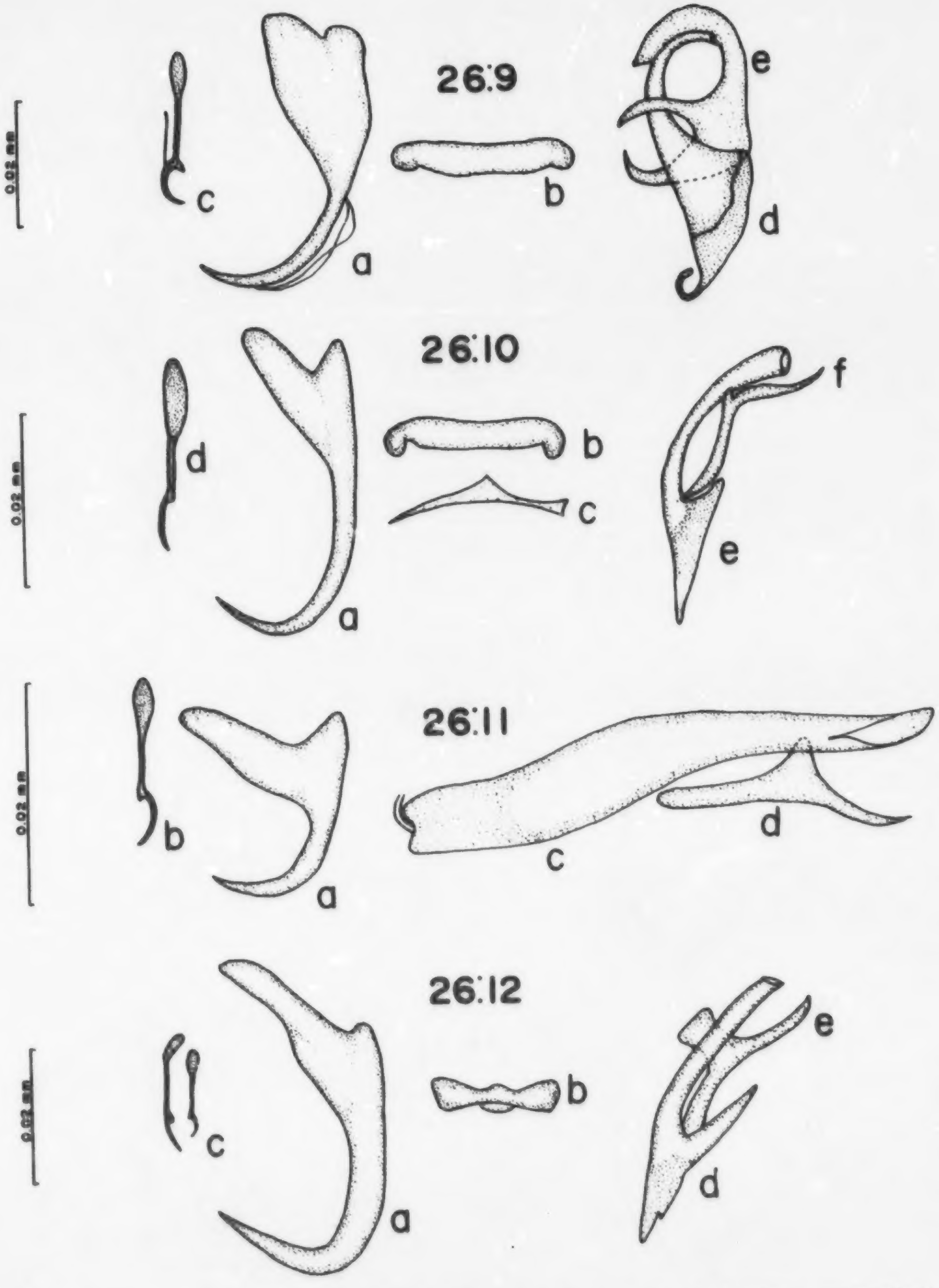
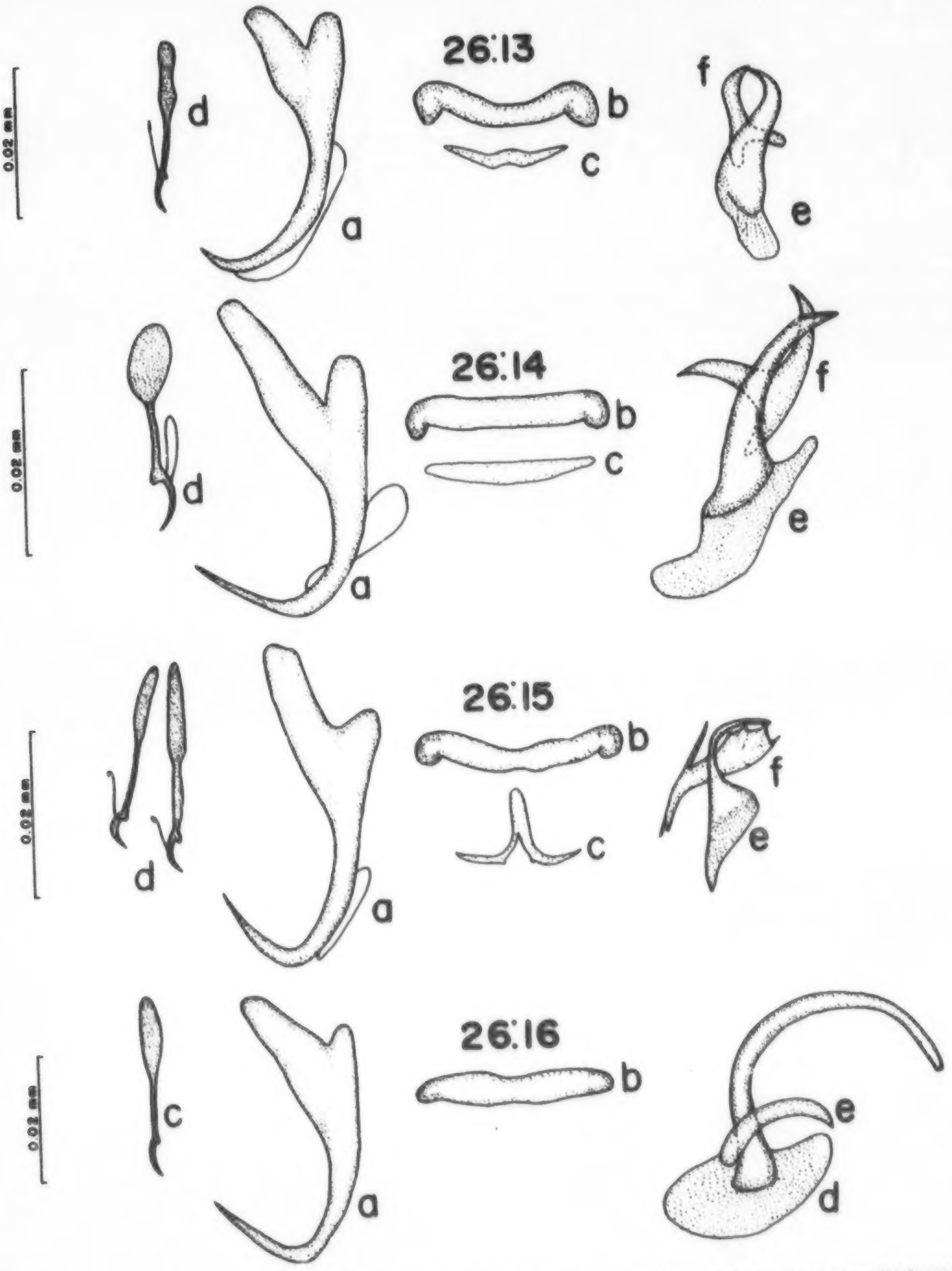

26:9
a
b
c
d
e
0.02 mm
26:10
a
b
c
d
e
f
0.02 mm
26:11
a
b
c
d
0.02 mm
26:12
a
b
c
d
e
0.02 mm

FIG. 26:9–26:12. *Dactylogyrus* spp. 26:9. *D. buddi* (modified from Dechtiar 1974b): a. hamulus; b. dorsal bar; c. marginal hook; d. penis; e. accessory piece. 26:10. *D. bulbus* (a–d modified from Mueller 1938, e,f from Mizelle and Donahue 1944): a. hamulus; b. dorsal bar; c. vestigial ventral bar; d. marginal hook; e. penis; f. accessory piece. 26:11 *D. bullosus* (modified from Mizelle and Donahue 1944): a. hamulus; b. marginal hook; c. penis; d. accessory piece (figures of bar(s) not available). 26:12. *D. bychowski* (modified from Mizelle 1938): a. hamulus; b. dorsal bar; c. marginal hooks; d. penis; e. accessory piece.


26:13
0.02 mm
a
b
c
d
e
f
26:14
0.02 mm
a
b
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d
d
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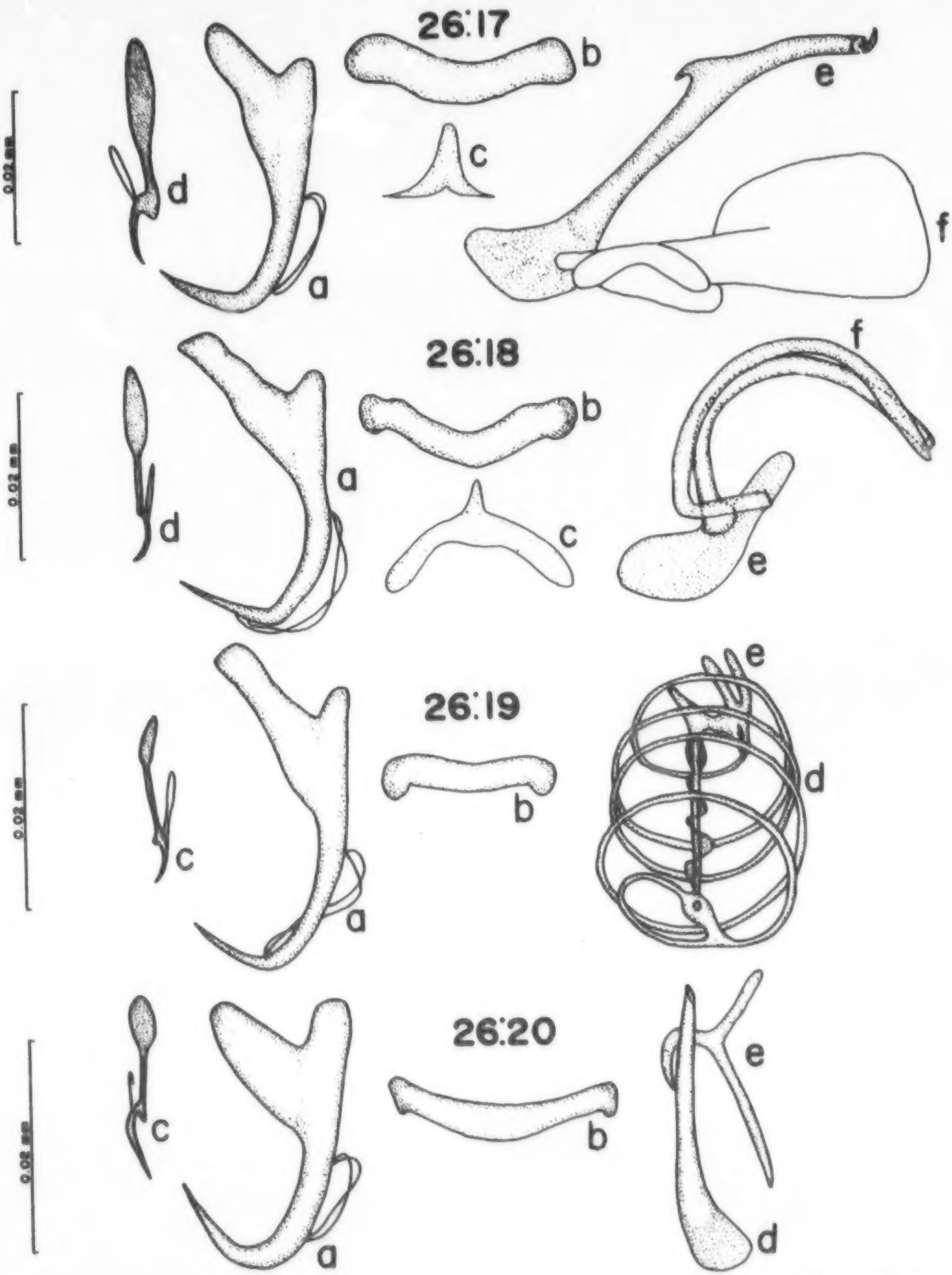
26:15
0.02 mm
a
b
c
d
e
f
26:16
0.02 mm
a
b
c
d
e

FIG. 26:13–26:16. *Dactylogyrus* spp. 26:13. *D. cheloideus* (modified from Rogers 1967b): a. hamulus; b. dorsal bar; c. vestigial ventral bar; d. marginal hook; e. penis; f. accessory piece. 26:14. *D. chrosomi* (modified from Hanek et al. 1975): a. hamulus; b. dorsal bar; c. vestigial ventral bar; d. marginal hook; e. penis; f. accessory piece. 26:15. *D. columbiensis* (modified from Monaco and Mizelle 1955): a. hamulus; b. dorsal bar; c. vestigial ventral bar; d. marginal hooks; e. penis; f. accessory piece. 26:16. *D. cornutus* (a–c modified from Mueller 1938, d,e from Mizelle and Donahue 1944): a. hamulus; b. dorsal bar; c. marginal hook; d. penis; e. accessory piece.


26:17
a
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c
d
e
f
0.02 mm
26:18
a
b
c
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f
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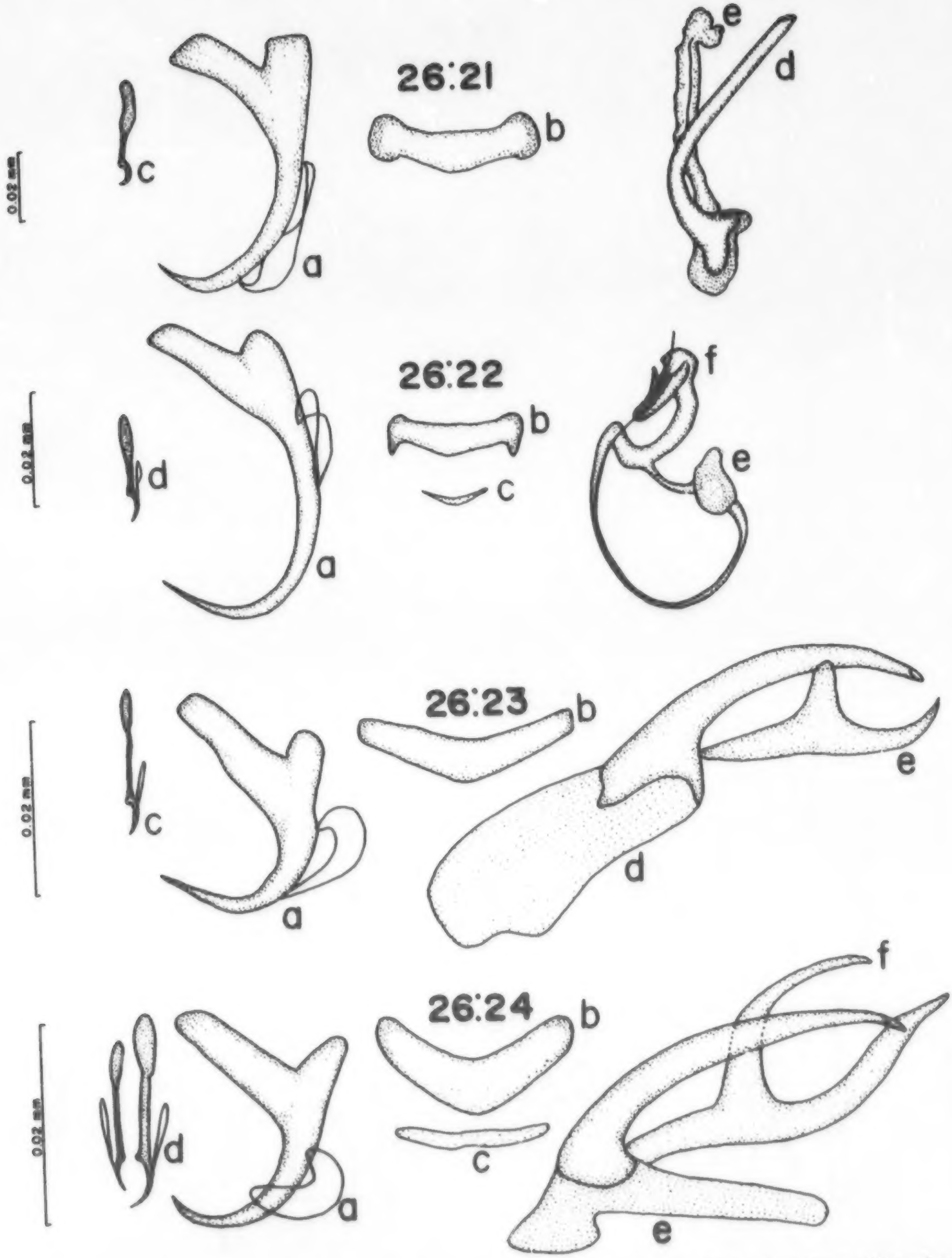
26:19
a
b
c
d
e
0.02 mm
26:20
a
b
c
d
e
0.02 mm

FIG. 26:17–26:20. *Dactylogyrus* spp. 26:17. *D. corporalis* (modified from Putz and Hoffman 1964): a. hamulus; b. dorsal bar; c. vestigial ventral bar; d. marginal hook; e. penis; f. accessory piece. 26:18. *D. dubius* (modified from Rogers 1967b): a. hamulus; b. dorsal bar; c. vestigial ventral bar; d. marginal hook; e. penis; f. accessory piece. 26:19. *D. eos* (modified from Hanek et al. 1975): a. hamulus; b. dorsal bar; c. marginal hook; d. penis; e. accessory piece. 26:20. *D. eucalius* (modified from Mizelle and Regensberger 1945): a. hamulus; b. dorsal bar; c. marginal hook, d. penis; e. accessory piece.



26:21
0.02 mm
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b
c
d
e
26:22
0.02 mm
a
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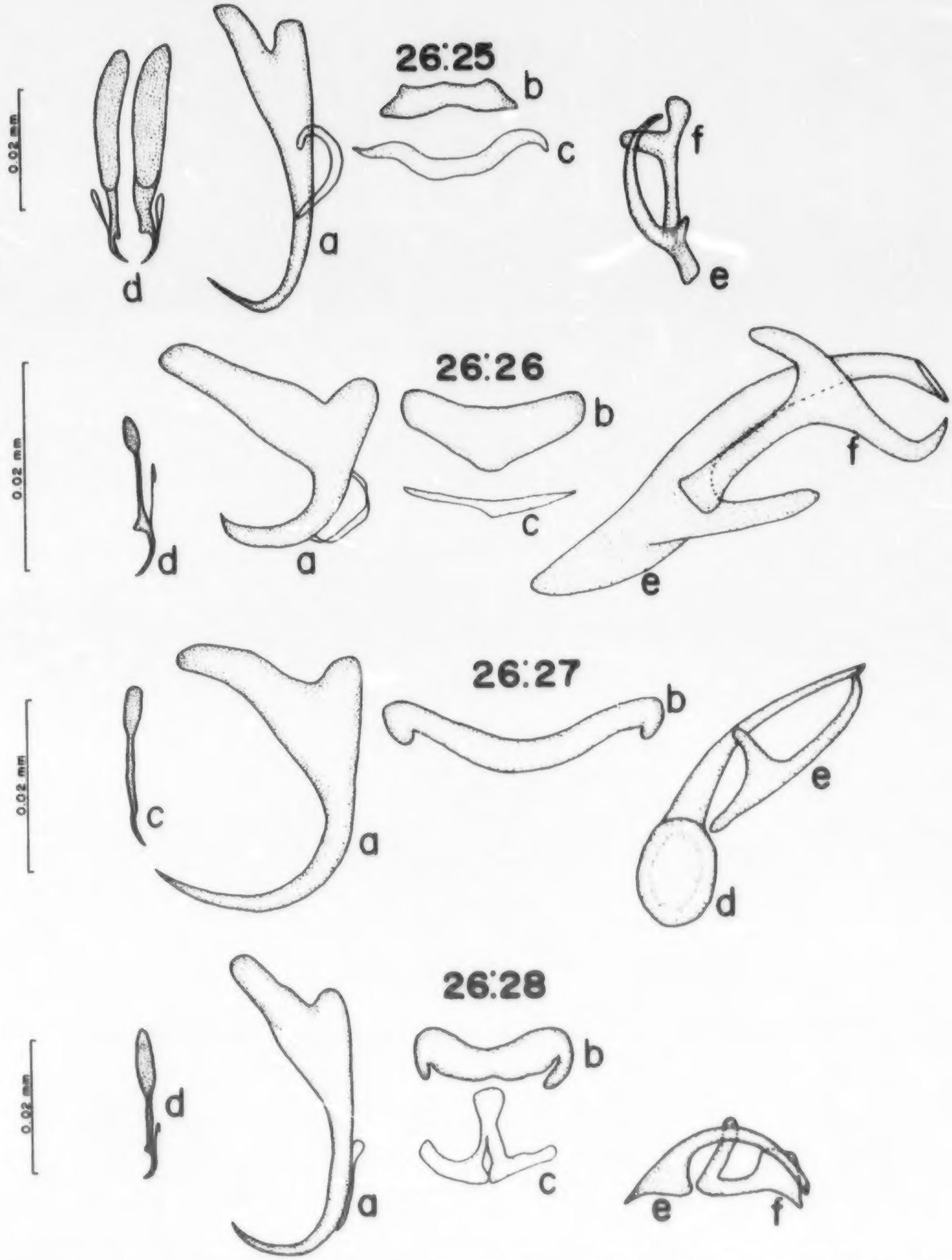
26:23
0.02 mm
a
b
c
d
e
26:24
0.02 mm
a
b
c
d
e
f

FIG. 26:21–26:24. *Dactylogyrus* spp. 26:21. *D. extensus* (a. modified from Ogawa and Egusa 1979, b–e from Gusev 1955): a. hamulus; b. dorsal bar; c. marginal hook; d. penis; e. accessory piece. 26:22 *D. flagristylus* (modified from Chien 1974b): a. hamulus; b. dorsal bar; c. vestigial ventral bar; d. marginal hook; e. penis; f. accessory piece. 26:23. *D. hankinsoni* (modified from Hanek et al. 1975): a. hamulus; b. dorsal bar; c. marginal hook; d. penis; e. accessory piece. 26:24. *D. heterolepis* (modified from Hanek et al. 1975): a. hamulus; b. dorsal bar; c. vestigial ventral bar; d. marginal hooks; e. penis; f. accessory piece.


26:25
0.02 mm
d
a
b
c
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e
26:26
0.02 mm
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b
c
f
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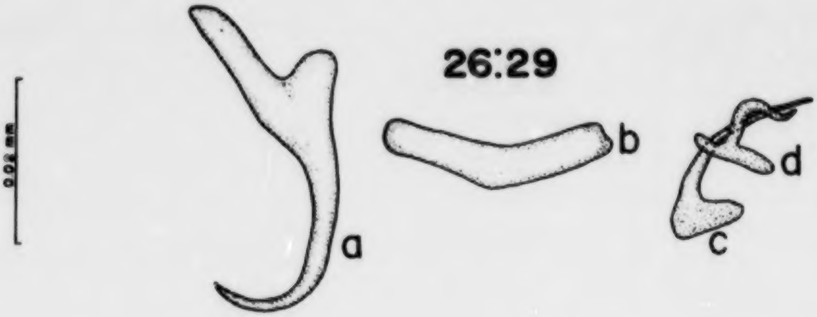
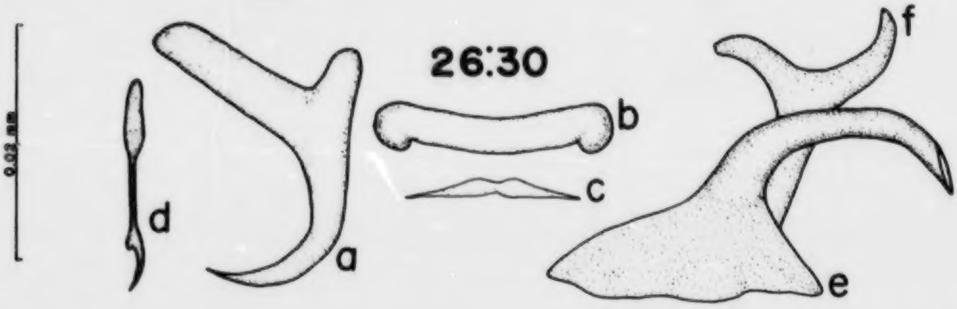
26:27
0.02 mm
c
a
b
e
d
26:28
0.02 mm
d
a
b
c
e
f

FIG. 26:25–26:28. *Dactylogyrus* spp. 26:25. *D. lachneri* (modified from Chien 1971): a. hamulus; b. dorsal bar; c. vestigial ventral bar; d. marginal hooks; e. penis; f. accessory piece. 26:26. *D. luxili* (modified from Rogers 1967b): a. hamulus; b. dorsal bar; c. vestigial ventral bar; d. marginal hook; e. penis; f. accessory piece. 26:27. *D. microphallus* (modified from Mueller 1938): a. hamulus; b. dorsal bar; c. marginal hook; d. penis; e. accessory piece. 26:28. *D. mylocheilus* (modified from Monaco and Mizelle 1955): a. hamulus; b. dorsal bar; c. vestigial ventral bar; d. marginal hook; e. penis; f. accessory piece.

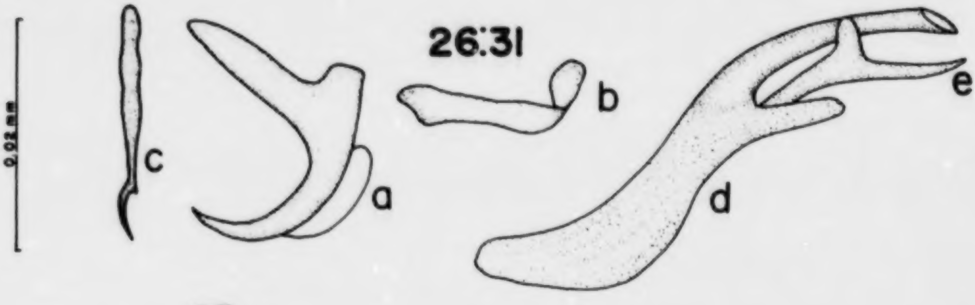
26:29



26:30



26:31



26:32

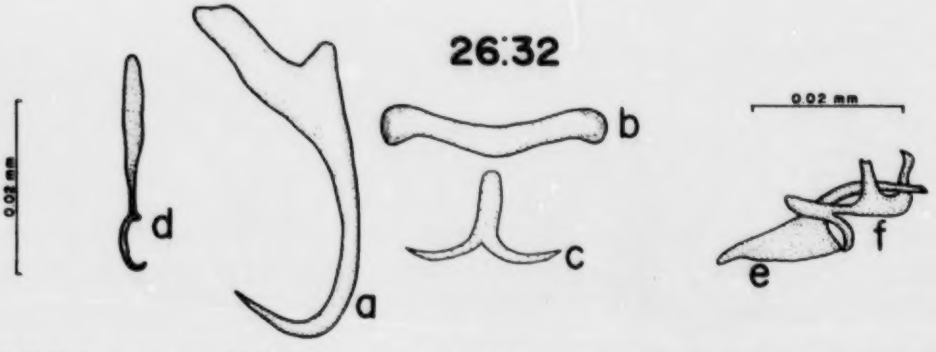
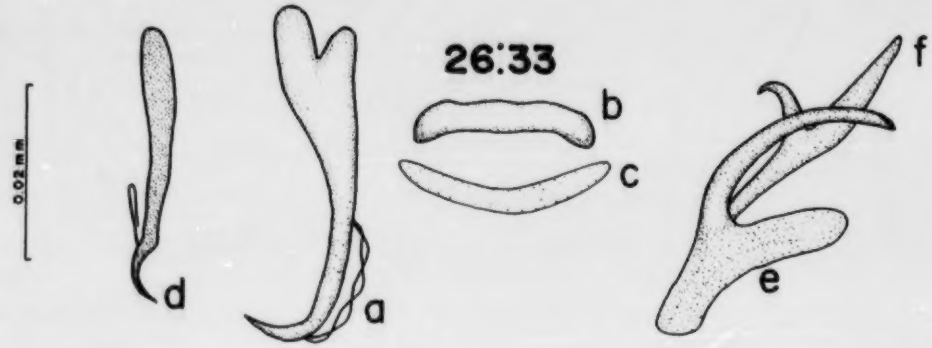
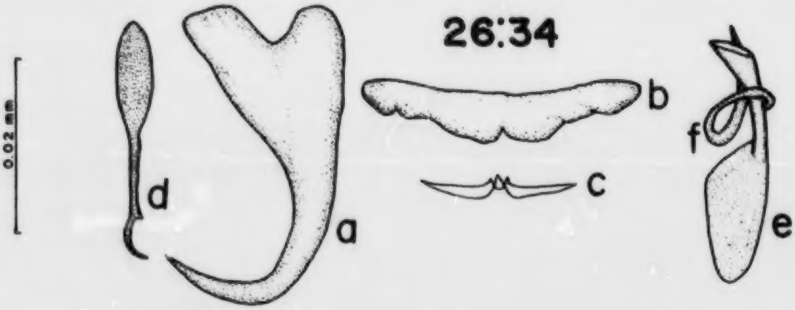


FIG. 26:29–26:32. *Dactylogyrus* spp. 26:29. *D. parvicirrus* (c,d modified from Seamster 1948, a, b from Hargis 1953): a. hamulus; b. dorsal bar; c. penis; d. accessory piece (figure of marginal hook not available). 26:30. *D. perlus* (modified from Mueller 1938): a. hamulus; b. dorsal bar; c. vestigial ventral bar; d. marginal hook; e. penis; f. accessory piece. 26:31. *D. pollex* (modified from Mizelle and Donahue 1944): a. hamulus; b. dorsal bar; c. marginal hook; d. penis; e. accessory piece. 26:32. *D. ptychocheilus* (modified from Monaco and Mizelle 1955): a. hamulus; b. dorsal bar; c. vestigial ventral bar; d. marginal hook; e. penis; f. accessory piece.

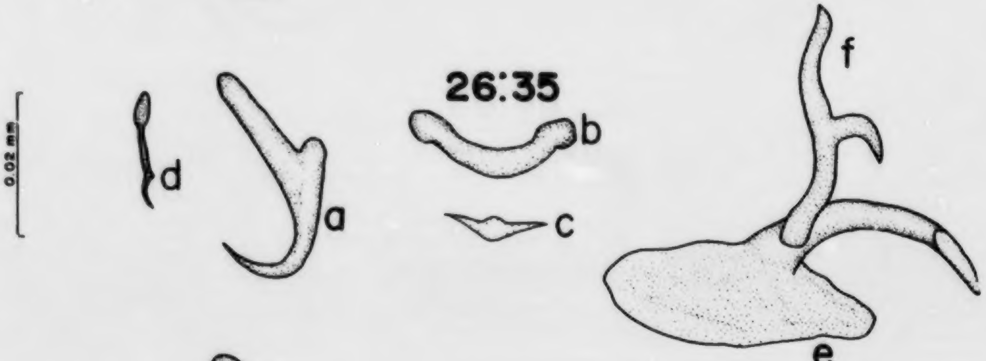
26:33



26:34



26:35



26:36

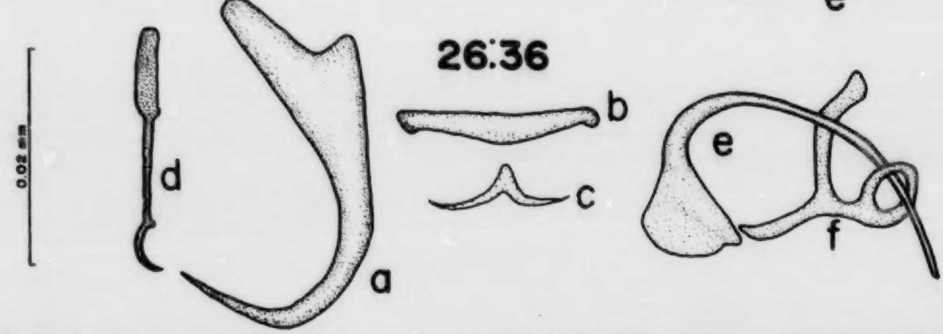
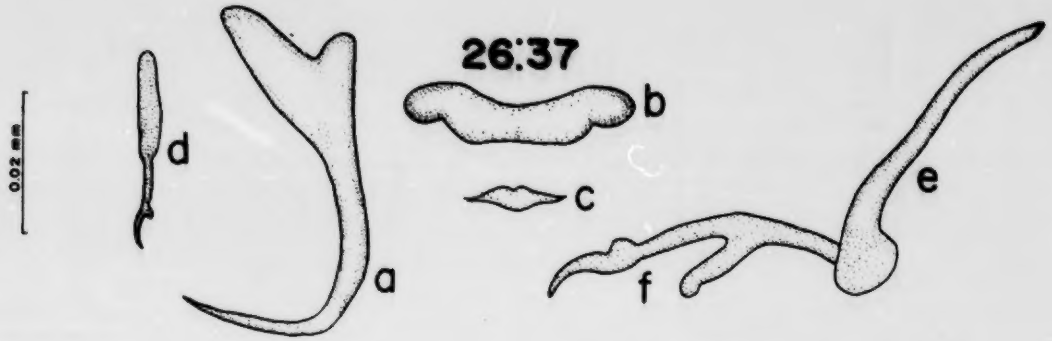
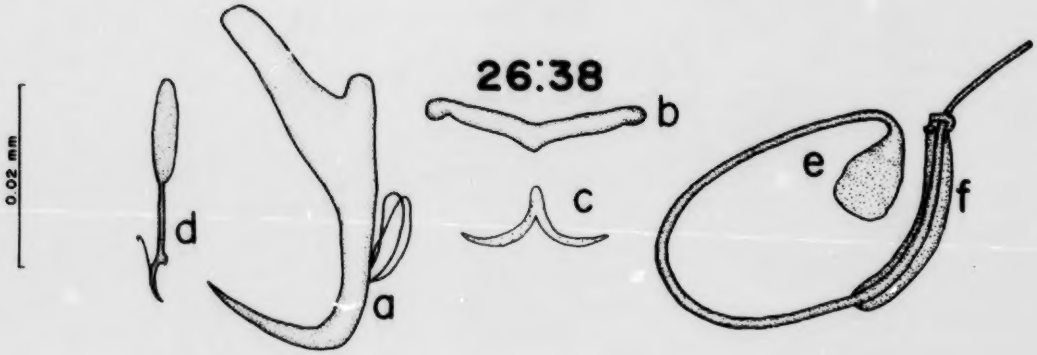


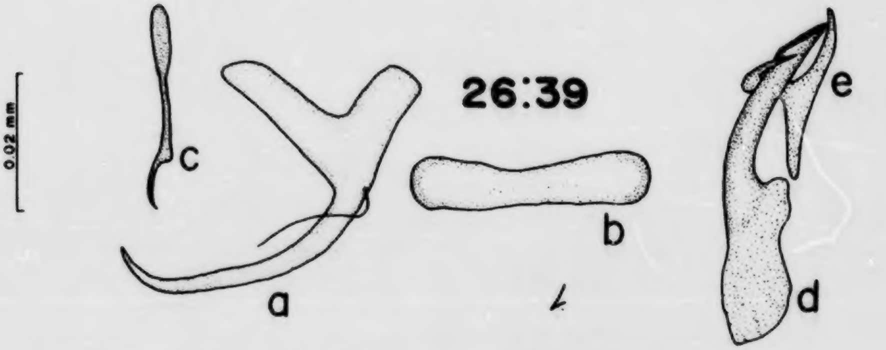
FIG. 26:33–26:36. *Dactylogyrus* spp. 26:33. *D. reciprocus* (modified from Rogers 1967b): a. hamulus; b. dorsal bar; c. vestigial ventral bar; d. marginal hook; e. penis; f. accessory piece. 26:34. *D. richardsonius* (modified from Monaco and Mizelle 1955): a. hamulus; b. dorsal bar; c. vestigial ventral bar; d. marginal hook; e. penis; f. accessory piece. 26:35. *D. rubellus* (modified from Mueller 1938): a. hamulus; b. dorsal bar; c. vestigial ventral bar; d. marginal hook; e. penis; f. accessory piece. 26:36. *D. tridactylus* (modified from Monaco and Mizelle 1955): a. hamulus; b. dorsal bar; c. vestigial ventral bar; d. marginal hook; e. penis; f. accessory piece.



26:37



26:38



26:39

FIG. 26:37–26:39. *Dactylogyrus* spp. 26:37. *D. urus* (modified from Mueller 1938): a. hamulus; b. dorsal bar; c. vestigial ventral bar; d. marginal hook; e. penis; f. accessory piece. 26:38. *D. vancleavei* (modified from Monaco and Mizelle 1955): a. hamulus; b. dorsal bar; c. vestigial ventral bar; d. marginal hook; e. penis; f. accessory piece. 26:39. *D. vastator* (modified from Bykhovskaya-Pavlovskaya et al. 1962): a. hamulus; b. dorsal bar; c. marginal hook; d. penis; e. accessory piece.

TABLE 13. Comparative measurements (in μm) of the species of *Dactylogyrus* Diesing, 1850, recorded from *Carassius auratus*, *Chrosomus eos*, *Cyprinus carpio*, and *Hybognathus hankinsoni* (Cyprinidae) of Canada.

Species	*D. anchoratus*	*D. vastator*	*D. chrosomi*	*D. eos*	*D. extensus*	*D. hankinsoni*
Source of data	Price and Mizelle (1964)	Bykhovskaya-Pavlovskaya et al. (1962)	Hanek et al. (1975)	Hanek et al. (1975)	Mizelle and Klucka (1953)	Hanek et al. (1975)
Body: length	"about" 349 (326–388)	362 (328–388)[a]	540 (400–580)	250 (230–280)	1296 (990–1584)	600 (440–710)
width	97 (79–116)	81 (72–90)[a]	170 (140–200)	75 (52–100)	158 (126–180)	135 (90–156)
Hamuli: length	96 (88–101)	35–41	28 (27–29)	32 (31–33)	81 (75–88)	23 (22–24)
Dorsal bar: transverse length	23 (22–24)	32–38	20 (19–21)	17 (16–18)	47 (42–50)	22 (20–23)
Ventral bar: transverse length	—	—	14	—	—	—
Marginal hooks: total length	19 (13–25)	29–35	19 (17–22)	18 (13–21)	31–35	15 (14–17)
Penis: length	23 (21–25)	44–58	22 (21–23)	27 (24–30)	71 (54–83)	32 (30–35)
Accessory piece: length	16 (15–17)	—	15 (14–16)	26 (24–28)	55 (42–71)	24 (23–26)
Site(s)	gills	gills	gills	gills	gills, fins	gills
Host(s)	*Carassius auratus* *Cyprinus carpio*	*Carassius auratus*	*Chrosomus eos*	*Chrosomus eos*	*Cyprinus carpio*[b] *Micropterus dolomieui*	*Hybognathus hankinsoni*
Locality(ies)	British Columbia Ontario	Ontario	Ontario	New Brunswick Ontario	British Columbia Nova Scotia Ontario	Ontario

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[a] From Price and Mizelle (1964); measurements for haptoral components by these authors fall within the range given by Bykhovskaya-Pavlovskaya et al. (1962).

[b] See remarks on *D. extensus* on p. 96.

TABLE 14. Comparative measurements (in μm) of the species of *Dactylogyrus* Diesing, 1850, recorded from *Mylocheilus caurinus*, *Notemigonus crysoleucas*, *Pimephales* spp., and *Platygobio gracilis* (Cyprinidae) of Canada.

Species	*D. mylocheilus*	*D. aureus*	*D. parvicirrus*	*D. bifurcatus*	*D. bychowskyi*	*D. albertensis*
Source of data	Monaco and Mizelle (1955)	Hanek and Fernando (1972b)	Seamster (1948)	Mizelle (1937)	Mizelle (1937)	Price and Arai (1967)
Body: length	414 (324–486)	572–590	224 (180–270)	343 (254–492)	381 (285–615)	468 (441–521)
width	79 (54–108)	95–108	63 (47–82)	70 (49–95)	79 (49–108)	85 (75–91)
Hamuli: length	46 (45–49)	24–25	38 (36–41)	33 (28–34)	48 (38–57)	37 (35–39)
Dorsal bar: transverse length	26 (23–29)	24–26	30 (25–34)	17 (15–23)	21 (17–25)	30 (28–33)
Ventral bar: transverse length	22 (20–25)	—	—	—[a]	—	"vestigial"
Marginal hooks: total length	23 (20–27)	14–17	19–24	13–23	11–21	21–28
Penis: length	24 (20–27)	42–50	13 (11–16)	29 (27–30)	44 (38–51)	38 (35–40)
Accessory piece: length	15 (14–16)	40–44	8 (7–9)	Distally bifurcate	—	23 (21–25)
Site	gills	gills	gills	gills	gills	gills
Host(s)	*Couesius plumbeus* *Mylocheilus caurinus*[b]	*Notemigonus crysoleucas*	*Notemigonus crysoleucas*	*Pimephales notatus* *P. promelas*	*Pimephales notatus* *P. promelas*	*Platygobio gracilis*
Locality(ies)	British Columbia Manitoba Ontario	Ontario	New Brunswick Manitoba Ontario	Manitoba Ontario	Ontario	Alberta

[a] Approximately the same length as the dorsal bar (Mizelle 1937).
[b] Type host.

TABLE 15. Comparative measurements (in μm) of the species of *Dactylogyrus* Diesing, 1850, recorded from *Nocomis micropogon* (Cyprinidae) of Canada.

Species	*D. aviunguis*[a]	*D. flagristylus*	*D. lachneri*	*D. reciprocus*
Source of data	Hanek et al. (1975)	Chien (1974b)	Chien (1971)	Rogers (1967b)
Body: length	300 (210–330)	235 (140–340)	275 (160–400)	365 (220–490)
width	69 (59–90)	85 (50–120)	91 (48–138)	84 (40–100)
Hamuli: length	28 (25–33)	53 (45–61)	52 (32–64)	40 (31–45)
Dorsal bar: transverse length	21 (18–26)	28 (24–34)	27 (23–33)	21 (17–25)
Ventral bar: transverse length	16 (15–17)	15 (13–17)	35 (23–47)	25 (20–30)
Marginal hooks: total length	15–27	21 (16–29)	18–43	18–40
Penis: length	18 (17–19)	"whip-like"	30 (20–43)	43 (32–56)
Accessory piece: length	15 (13–16)	39 (28–45)	37 (20–46)	32 (24–37)
Site	gills	gills	gills	gills
Host	*Nocomis micropogon*	*Nocomis micropogon*	*Nocomis micropogon*	*Nocomis micropogon*
Locality	Ontario	Ontario	Ontario	Ontario

[a] As *D. micropogoni*, which was declared a synonym of *D. aviunguis* by Kritsky et al. (1977).

TABLE 16. Comparative measurements (in μm) of the species of *Dactylogyrus* Diesing, 1850, recorded from *Notropis* spp. (Cyprinidae) of Canada.

Species	*D. banghami*	*D. bulbus*	*D. bullosus*	*D. cornutus*	*D. dubius*	*D. luxili*	*D. perlus*	*D. pollex*	*D. heterolepis*	*D. rubellus*
Source of data	Mizelle and Donahue (1944)	Mizelle and Donahue (1944)	Mizelle and Donahue (1944)	Mizelle and Webb (1953)	Hanek et al. (1975)	Rogers (1967b)	Mizelle and Donahue (1944)	Mizelle and Donahue (1944)	Hanek et al. (1975)	Mueller (1938)
Body: length	294 (270–350)	306 (270–342)	360	423 (406–435)	685 (530–850)	326 (215–390)	273	306	460 (325–580)	300–370
width	78 (60–82)	56 (47–69)	95	99 (71–126)	157 (110–195)	86 (60–110)	69	77	112 (65–150)	—
Hamuli: length	20 (16–22)	36	19	38 (34–42)	35 (32–38)	19 (18–19)	25	20	20 (18–22)	32
Dorsal bar: transverse length	20 (19–21)	18	38	31 (30–32)	29 (23–32)	17 (16–18)	24	18	20 (18–25)	25
Ventral bar: transverse length	14	20	—	24	23 (18–28)	16 (14–17)	—	—	16 (15–18)	18
Marginal hooks: total length	12–18	20–25	13–18	16–20[b]	21 (19–25)	15 (12–17)	11–15	14–19	19 (16–21)	16
Penis: length	36 (34–38)	31 (20–40)	50	48 (42–50)	34 (24–40)	40 (34–42)	31	41	36 (32–39)	50
Accessory piece: length	24 (22–27)	28 (26–29)	23	16 (12–19)	30 (24–32)	23 (22–25)	—	22	33 (28–36)	34
Site	gills	gills	gills	gills	gills	gills	gills	gills	gills	gills
Host(s)	*Couesius plumbeus*[a] *Notropis cornutus*[c] *Rhinichthys atratulus* *R. cataractae* *Richardsonius balteatus*	*Notropis cornutus*[c] *N. crysoleucas*	*Notropis cornutus*	*Notropis cornutus*	*Notropis cornutus*[c] *Semotilus atromaculatus*	*Notropis cornutus*	*Notropis cornutus*	*Notropis cornutus*	*Notropis heterolepis*	*Notropis rubellus*
Locality(ies)	Alberta British Columbia Manitoba Ontario	New Brunswick Ontario	Ontario	Ontario	New Brunswick Ontario	Ontario	Ontario	Ontario	Ontario	Ontario

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[a] See remarks on *D. banghami* on p. 98.
[b] From Mizelle and Donahue (1944).
[c] Type host.

TABLE 17. Comparative measurements (in µm) of the species of *Dactylogyrus* Diesing, 1850, recorded from *Acrocheilus alutaceus*, *Ptychocheilus oregonensis*, *Rhinichthys atratulus*, *Richardsonius balteatus* and *Semotilus* spp. (Cyprinidae) of Canada.

Species	*D. columbiensis*	*D. ptychocheilus*	*D. tridactylus*	*D. vancleavei*	*D. cheloideus*	*D. richardsonius*	*D. attenuatus*	*D. microphallus*	*D. corporalis*
Source of data	Monaco and Mizelle (1955)	Monaco and Mizelle (1955)	Monaco and Mizelle (1955)	Monaco and Mizelle (1955)	Rogers (1967b)	Monaco and Mizelle (1955)	Mizelle and Klucka (1953)	Mizelle and Klucka (1953)	Putz and Hoffman (1964)
Body: length	360	309 (234–414)	270–306	367 (198–432)	380 (310–470)	558 (378–684)	269 (250–288)	336 (270–414)	800 (575–1062)
width	54	72 (54–108)	72–90	92 (54–144)	75 (65–90)	245 (198–306)	78 (72–90)	75 maximum	110 (75–125)
Hamuli: length	38	41 (40–45)	31–32	38 (36–40)	37 (36–38)	32 (29–34)	41 (38–46)	32 (29–33)	42 (38–43)[a]
Dorsal bar: transverse length	25	25 (22–27)	22–23	22 (20–23)	27 (25–28)	29 (25–32)	32 (31–33)	26 (25–27)	29 (23–33)
Ventral bar: transverse length	18	16 (14–18)	13	12 (11–13)	16 (14–17)	17 (14–20)	24	—	12[b]
Marginal hooks: total length	22–23	23 (18–27)	18–23	22 (18–25)	18–27	23 (22–25)	22	18–22	28
Penis: length	18	26 (23–29)	20–22	"long tube"	26 (25–27)	22 (20–23)	27 (25–29)	36 (35–38)	68 (53–79)
Accessory piece: length	18	15 (12–18)	14–16	"long tube-like"	13 (12–14)	11 (10–12)	17 (16–18)	25 (24–26)	60 (50–70)
Site	gills	gills	gills	gills	gills	gills	gills	gills	gills
Host(s)	*Ptychocheilus oregonensis*	*Ptychocheilus oregonensis*	*Ptychocheilus oregonensis*	*Acrocheilus alutaceus* *Ptychocheilus oregonensis*[c]	*Rhinichthys atratulus*	*Richardsonius balteatus*	*Semotilus atromaculatus*	*Semotilus atromaculatus*	*Semotilus corporalis*
Locality	British Columbia	British Columbia	British Columbia	British Columbia	Ontario	British Columbia	Ontario	Ontario	New Brunswick

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[a] "solid shaft 42 (38–43) long".

[b] "Tripartite with all parts approximately equal", 12 µm long.

[c] Presumed type host.

TABLE 18. Comparative measurements (in μm) of the species of *Dactylogyrus* Diesing, 1850, recorded from catostomids, a gasterosteid and cottids of Canada.

Species	*D. apos*	*D. urus*	*D. eucalius*	*D. buddi*
Source of data	Mueller (1938)	Mueller (1938)	Mizelle and Regensberger (1945)	Dechtiar (1974b)
Body: length	444	500	288 (180–360)	595 (415–634)
width	70	125	90 (43–138)	195 (98–224)
Hamuli: length	48	50	28 (25–31)	45 (40–50)
Dorsal bar: transverse length	32	30	31 (29–36)	34 (29–37)
Ventral bar: transverse length	14	14	—	—
Marginal hooks: total length	28	30	16–22	24–32
Penis: length	"robust"	50	29 (25–32)	38 (32–44)
Accessory piece: length	"3 arms"	—	22 (20–24)	28 (24–32)
Site	gills	gills	gills	gills
Host(s)	*Hypentelium nigricans*	*Moxostoma anisurum* *M. erythrurum*	*Culaea inconstans*	*Cottus bairdi* *C. cognatus*
Locality(ies)	Ontario	Manitoba Ontario	Manitoba Ontario	Ontario Yukon Territory

8 Hamuli 40 long or less; ventral bar with median anterior projections; vagina latero-ventral, left .... *D. vancleavei* Monaco and Mizelle, 1955 (Fig. 26:38, Table 17)

On gills of *Acrocheilus alutaceus* (1); *Ptychocheilus oregonensis* (1,2)
Records: 1. Monaco and Mizelle 1955 (BC); 2. Anon. 1981 (BC)

Hamuli 45 long or more; ventral bar bowed posteriorly lacking median projection; vagina latero-ventral, right .... *D. flagristylus* Chien, 1974 (Fig. 26:22, Table 15)

On gills of *Nocomis micropogon*
Record: Hanek et al. 1975 (Ont)
Remarks: Recorded as *D. cernyi* by Hanek et al. (1975) — see Margolis and Arthur (1979)

9 Penis strongly curved with conspicuously inflated base. On *Notropis* spp. 20

Penis less strongly curved, base moderately inflated. Not on *Notropis* spp. 11

10 Accessory piece 12–19 long .... *D. cornutus* Mueller, 1938 (Fig. 26:16, Table 16)

On gills of *Notropis cornutus*
Records: Mizelle and Donahue 1944 (Ont); Molnar et al. 1974 (Ont); Hanek et al. 1975 (Ont)

Accessory piece 24–32 long .... *D. dubius* Mizelle and Klucka, 1953 (Fig. 26:18, Table 16)

On gills of *Notropis cornutus* (1,2); *Semotilus atromaculatus* (3)
Records: 1. Molnar et al. 1974 (Ont); 2. Hanek et al. 1975 (Ont); 3. Cone 1980 (NB)
Remarks: Guaev (1955) proposed *Dactylogyrus dubius* for a species found on the Khanka gudgeon (*Gnathopogon chankaensis*) in the USSR. The two species appear to be distinct and the North American form is thus the senior homonym and should retain the designation *D. dubius*. However, the validity of Mizelle and Klucka's (1953) species requires confirmation as it was based on a fragment of one specimen.

11 Hamuli 75–88 long; dorsal bar 42–50 transverse length; ventral bar apparently lacking. On *Cyprinus carpio* .... *D. extensus* Mueller and Van Cleave, 1932 (Fig. 26:21, Table 13)

On gills and fins of *Cyprinus carpio* (1,2,3,4,5); ?*Micropterus dolomieui* (1)

Records: 1. Fantham and Porter 1948 (NS); 2. Bangham and Adams 1954 (BC); 3. Bangham 1955 (Ont); 4. Monaco and Mizelle 1955 (BC); 5. Dechtiar 1972b (Ont)

Remarks: Although Fantham and Porter (1948) recorded *M. dolomieui* as a host of *D. extensus* it appears that the parasite has a high degree of specificity for *C. carpio*. Thus, *M. dolomieui* is regarded as an accidental host (or an incorrect identification).

Hamuli 38–49 long; dorsal bar 23–33 transverse length; ventral bar present. Not on *C. carpio* 12

12 Body 575–1062 long; penis 53–79 long; accessory piece 50–70 long, membranous, cradle-like with ringed distal aperture; ventral bar 12 transverse length .... *D. corporalis* Putz and Hoffman, 1964 (Fig. 26:17, Table 17)

On gills of *Semotilus corporalis*

Record: Cone 1980 (NB)

Body 324–486 long; penis 20–27 long, accessory piece 14–16 long, inflated distally to enclose tip of penis; ventral bar 20–25 transverse length .... *D. mylocheilus* Monaco and Mizelle, 1955 (Fig. 26:28, Table 14)

On gills of *Couesius plumbeus* (1,2,3); *Mylocheilus caurinus* (1)

Records: 1. Monaco and Mizelle 1955 (BC); 2. Dechtiar 1972c (Ont); 3. Lubinsky and Loch 1979 (Man)

13 Hamuli 88–101 long, "gyrodactyloid": superficial root elongate, deep root reduced (almost lacking) .... *D. anchoratus* (Dujardin, 1845) Wegener, 1857 (Fig. 26:2, Table 13)

On gills of *Carassius auratus* (2); *Cyprinus carpio* (1,2)

Records: 1. Monaco and Mizelle 1955 (BC); 2. Dechtiar 1972b (Ont)

Hamuli less than 65 long, "dactylogyroid": superficial root not conspicuously elongate, deep root measurable 14

14 Proximal part of hamuli distinctively Y-shaped with deep root almost as long as superficial root; angle of shaft and superficial root almost 90° .... *D. vastator* Nybelin, 1924 (Fig. 26:39, Table 13)

On gills of *Carassius auratus*

Record: Dechtiar 1972b (Ont)

Proximal part of hamuli more V-shaped with deep root shorter than superficial root; angle of shaft and superficial root obtuse 15

15 Ventral bar present, triradiate with distinct anterior projection. On *Ptychocheilus* spp. 16

Ventral bar apparently absent or, if present, not triradiate. Not on *Ptychocheilus* spp. 18

16 Diameter of base of penis about equal to length of tubular, distal region; ventral bar with anterior projection about as long as lateral projections 17

Diameter of base of penis comparatively narrow, about ¼ of length of tubular, distal region; ventral bar with anterior projection about ½ as long as lateral projections .... *D. tridactylus* Monaco and Mizelle, 1955 (Fig. 26:36, Table 17)

On gills of *Ptychocheilus oregonensis*
Record: Monaco and Mizelle 1955 (BC)
Remarks: Monaco and Mizelle (1955) proposed three species from *Ptychocheilus oregonensis* taken in British Columbia: *D. columbiensis*, *D. ptychocheilus*, and *D. tridactylus* based on one, 20, and two specimens, respectively. Monaco and Mizelle (1955) noted that *D. columbiensis* and *D. tridactylus* were closely related and considered the shape of the accessory piece, vagina, and ventral bar to be distinctive. However, the figures provided by Monaco and Mizelle (1955) are small and it is difficult to pinpoint morphological differences in these morphometrically similar species. All three species are included in the present key but further examination of material from *P. oregonensis* may result in synonymy.

17 Penis less than 20; hamuli less than 40 .... *D. columbiensis* Monaco and Mizelle, 1955 (Fig. 26:15, Table 17)
On gills of *Ptychocheilus oregonensis*
Record: Monaco and Mizelle 1955 (BC)
Remarks: See *D. tridactylus* above.

Penis more than 20; hamuli 40 or more .... *D. ptychocheilus* Monaco and Mizelle, 1955 (Fig. 26:32, Table 17)
On gills of *Ptychocheilus oregonensis*
Record: Monaco and Mizelle 1955 (BC)
Remarks: See *D. tridactylus* above.

18 Parasites of *Notropis*[46] spp. 19
Remarks: No less than 10 species of *Dactylogyrus* have been recorded from *Notropis* spp. in Canada, most of which are also present in the United States. They are:

D. banghami	Mizelle and Donahue (1944)
D. bulbus	Mueller (1938)
*D. bullosus**	Mizelle and Donahue (1944)
D. cornutus	Mueller (1938)
D. dubius	Mizelle and Klucka (1953)
*D. heterolepis**	Hanek et al. (1975)
D. luxili	Rogers (1967b)
D. perlus	Mueller (1938)
*D. pollex**	Mizelle and Donahue (1944)
D. rubellus	Mueller (1938)

*No record since original description.

Of the 10 species, four were proposed by Mueller (1938) and three by Mizelle and Donahue (1944). The paucity of data provided by Mueller (1938) suggests that he worked with a limited number of specimens as did Mizelle and Donahue (1944) who stated that *D. pollex* and *D. bullosus* were based on single worms and *D. banghami* on three. *D. dubius* was proposed for a *fragment* of one specimen (Mizelle and Klucka 1953).

In attempting to construct a key to *Dactylogyrus* spp. from Canadian fishes, host specificity has been used as a distinguishing character. Thus, species parasitizing *Notropis* spp. were grouped together and it is evident that several are similar. The penis "type" appears to be a wide-based, robust, curved penis with a triradiate accessory piece. It is suggested that reexamination of additional specimens will clarify the taxonomic status of these "species", some of which will probably be regarded as synonyms.

Parasites of cyprinids other than *Notropis* spp. 26

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[46] *Dactylogyrus banghami*, originally described from *N. cornutus*, is also reported from *Couesius plumbeus*, *Rhinichthys* spp. and *Richardsonius balteatus* — see remarks on *D. banghami* on p. 98.

19 **Penis curved with conspicuously inflated base** **20**

Penis less strongly curved with uninflated base[47] **25**

20 **Hamuli 25 long, or less, with superficial root/deep root junction an obtuse angle** **21**

Hamuli 30 long, or more, with superficial root/deep root junction a right angle **24**

21 **Dorsal bar robust with bowed posterior margin and uninflated lateral extremities; ventral bar straight, rod-like** **22**

Dorsal bar comparatively slender, lateral extremities with posterior inflations; ventral bar bowed or with median constriction **23**

22 **Dorsal bar conspicuously bowed along anterior margin; accessory piece 28–36 long** .... ***D. heterolepis* Hanek, Molnar and Fernando, 1975 (Fig. 26:24, Table 16)**
On gills of *Notropis heterolepis*
Record: Hanek et al. 1975 (Ont)

Dorsal bar slightly bowed along anterior margin, accessory piece 22–25 long .... ***D. luxili* Rogers, 1967 (Fig. 26:26, Table 16)**
On gills of *Notropis cornutus*
Record: Hanek et al. 1975 (Ont)

23 **Penis base with prominent distal projection; dorsal bar 19–21 transverse length** .... ***D. banghami* Mizelle and Donahue, 1944 (Fig. 26:7, Table 16)**
On gills of *Couesius plumbeus* (2); *Notropis cornutus* (1,2,7,8); *Rhinichthys atratulus* (5,8); *R. cataractae* (2,3,4,5,6,9); *Richardsonius balteatus* (2)
Records: 1. Mizelle and Donahue 1944 (Ont); 2. Monaco and Mizelle 1955 (BC, Ont); 3. Price and Arai 1967 (Alta); 4. Dechtiar 1972c (Ont); 5. Hanek and Fernando 1972b (Ont); 6. Arai and Chien 1973 (Alta); 7. Molnar et al. 1974 (Ont); 8. Hanek et al. 1975 (Ont); 9. Lubinsky and Loch 1979 (Man)
Remarks: *Dactylogyrus banghami* was based on specimens from *Notropis cornutus* taken in Ontario (Mizelle and Donahue 1944). Monaco and Mizelle (1955) listed *Couesius plumbeus, Rhinichthys cataractae* and *Richardsonius balteatus* as well as *N. cornutus* as hosts. Other North American records are those of Rogers (1967b) from eight *Notropis* spp., Price and Arai (1967) from *Rhinichthys cataractae*, and Hanek et al. (1975) from *N. cornutus* and *R. atratulus*. It is suggested that *D. banghami* is primarily a parasite of *Notropis* spp. and the other hosts are "accidental hosts" becoming infected by ecological association with *Notropis* spp.

Penis base lacking distal projection; dorsal bar 24 transverse length .... ***D. perlus* Mueller, 1938 (Fig. 26:30, Table 16)**
On gills of *Notropis cornutus*
Record: Mizelle and Donahue 1944 (Ont)

24 **Penis with distal inflation; penis and accessory piece 20–40 and 26–29 long, respectively; marginal hooks 20–25 long** .... ***D. bulbus* Mueller, 1938 (Fig. 26:10, Table 16)**
On gills of *Notemigonus crysoleucas* (4); *Notropis cornutus* (1,2,3,4)
Records: 1. Mizelle and Donahue 1944 (Ont); 2. Molnar et al. 1974 (Ont); 3. Hanek et al. 1975 (Ont); 4. Cone 1980 (NB)

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[47] **See remarks concerning *D. pollex* on p. 99.**

Penis lacking distal inflation; penis and accessory piece 50 and 34 long, respectively; marginal hooks 16 long .... *D. rubellus* Mueller, 1938 (Fig. 26:35, Table 16)
On gills of *Notropis rubellus*
Record: Hanek et al. 1975 (Ont)

25 Penis less than 45 long, with thumb-like projection near midlength; dorsal bar less than 20 transverse length .... *D. pollex* Mizelle and Donahue, 1944 (Fig. 26:31, Table 16)
On gills of *Notropis cornutus*
Record: Mizelle and Donahue 1944 (Ont)
Remarks: Mizelle and Donahue (1944) proposed *D. bullosus* and *D. pollex* from *Notropis cornutus* taken in Ontario. Both species were based on single specimens and neither has since been reported. The descriptions and figures of the copulatory complex provided by Mizelle and Donahue (1944) are confusing. Most *Dactylogyrus* spp. from *Notropis* spp. (and some other hosts) have a broad based penis and it is probable the thumb-like projection of *D. pollex* is part of the base and the "ovate perforation" of *D. bullosus* is the base reflected back on itself. Further observations are needed to clarify the penis/accessory piece morphology. The haptoral sclerites are similar in size although *D. bullosus* has a dorsal bar 38 in transverse length while that of *D. pollex* is stated to be 18. However, the bar is depicted with a fold so that the measurement of a straightened bar would be greater. It is suggested that *D. pollex* may prove to be a synonym of *D. bullosus* which in turn may prove to be identical with another, previously described, species occurring on *Notropis* spp.

Penis more than 45 long, lacking thumb-like projection; dorsal bar more than 35 transverse length .... *D. bullosus* Mizelle and Donahue, 1944 (Fig. 26:11, Table 16)
On gills of *Notropis cornutus*
Record: Mizelle and Donahue 1944 (Ont)
Remarks: See *D. pollex* above.

26 Parasites of *Nocomis micropogon* 27

Parasites of cyprinids other than *Nocomis micropogon* 29

27 Conspicuous ventral bar, longer than dorsal bar; marginal hooks up to 40 long (pair II) with inflated handle and short, thick shaft 28

Inconspicuous ventral bar, shorter than dorsal bar; marginal hooks up to 27 long (pair II) with inflated handle and distinct, slender shaft .... *D. aviunguis* Chien, 1974 (Fig. 26:6, Table 15)
On gills of *Nocomis micropogon*
Record: Hanek et al. 1975 (Ont)

28 Accessory piece (24–37 long) not as long as penis (32–56 long) ....
.... *D. reciprocus* Rogers, 1967 (Fig. 26:33, Table 15)
On gills of *Nocomis micropogon*
Record: Hanek et al. 1975 (Ont)

Accessory piece (20–46 long) as long as penis (20–43 long) ....
.... *D. lachneri* Chien, 1971 (Fig. 26:25, Table 15)
On gills of *Nocomis micropogon*
Record: Hanek et al. 1975 (Ont)

29 Parasites of *Semotilus* spp. 30

Parasites of cyprinids other than *Semotilus* spp. 31

30 Penis and accessory piece 35–38 and 24–26 long, respectively; hamuli 29–33 long ....
.... *D. microphallus* Mueller, 1938 (Fig. 26:27, Table 17)

On gills of *Semotilus atromaculatus*
Record: Hanek et al. 1975 (Ont)

Penis and accessory piece 25–29 and 16–18 long, respectively; hamuli 38–46 long ....
.... *D. attenuatus* Mizelle and Klucka, 1953 (Fig. 26:4, Table 17)

On gills of *Semotilus atromaculatus*
Records: Molnar et al. 1974 (Ont); Hanek et al. 1975 (Ont)

31 Parasites of *Notemigonus* spp. 32

Parasites of cyprinids other than *Notemigonus* spp. 33

32 Penis and accessory piece 11–16 and 7–9 long, respectively; hamuli 36–41 long[48] ....
.... *D. parvicirrus* Seamster, 1948 (Fig. 26:29, Table 14)

On gills of *Notemigonus chrysoleucas*
Records: Dechtiar 1972c (Ont); Lubinsky and Loch 1979 (Man); Cone 1980 (NB)

Penis and accessory piece 42–50 and 40–44 long, respectively; hamuli 24–25 long ....
.... *D. aureus* Seamster, 1948 (Fig. 26:5, Table 14)

On gills of *Notemigonus chrysoleucas*
Record: Hanek and Fernando 1972b (Ont)
Remarks: Further studies are needed to clarify the morphology of the copulatory apparatus which, according to Hargis (1953), carries a "second accessory piece". This structure, which arises at the proximal end of the penis, may be part of the inflated base (see figures of *D. albertensis, D. aviunguis, D. banghami,* and *D. bychowskyi*).

33 Parasites of *Pimephales* spp. 34

Parasites of cyprinids other than *Pimephales* spp. 35

34 Hamuli 38–57 long, with superficial root conspicuously longer than dorsal root ....
.... *D. bychowskyi* Mizelle, 1937 (Fig. 26:12, Table 14)

On gills of *Pimephales notatus* (2); *P. promelas* (1,2)
Records: 1. Molnar et al. 1974 (Ont); 2. Hanek et al. 1975 (Ont)

Hamuli 28–34 long, with superficial root about equal in length to dorsal root ....
.... *D. bifurcatus* Mizelle, 1937 (Fig. 26:8, Table 14)

On gills of *Pimephales notatus* (1,2,3); *P. promelas* (2)
Records: 1. Dechtiar 1972c (Ont); 2. Hanek et al. 1975 (Ont); 3. Lubinsky and Loch 1979 (Man)

35 Hamuli with superficial root conspicuously longer than deep root; penis with conspicuously inflated base. Parasites of *Chrosomus* spp. or *Hybognathus* spp. or *Platygobio* sp. 36

Hamuli with superficial root about equal in length to dorsal root; penis with slightly inflated base. Parasites of *Rhinichthys* sp. and *Richardsonius* sp. 38

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[48] From Seamster (1948). Hargis (1953) gave measurements of 18–28 and 10–16 long for the penis and accessory piece and 42–50 for the hamuli.

36 **Base of penis extended towards distal tip of penis; dorsal bar with posteriorly inflated extremities. On *Chrosomus* sp. or *Platygobio* sp.** 37

Base of penis not extended towards distal tip of penis; dorsal bar lacking inflated extremities. On *Hybognathus* sp. ...... ***D. hankinsoni* Hanek, Molnar and Fernando, 1975 (Fig. 26:23, Table 13)**
On gills of *Hybognathus hankinsoni*
Record: Hanek et al. 1975 (Ont)

37 **Penis and accessory piece 35–40 and 21–25 long, respectively; hamuli 35–39 long; dorsal bar bowed posteriorly** .... ***D. albertensis* Price and Arai, 1967 (Fig. 26:1, Table 14)**
On gills of *Platygobio gracilis*
Records: Price and Arai 1967 (Alta); Arai and Chien 1973 (Alta)

Penis and accessory piece 21–23 and 14–16 long, respectively; hamuli 27–29 long; dorsal bar straight .... ***D. chrosomi* Hanek, Molnar and Fernando, 1975 (Fig. 26:14, Table 13)**
On gills of *Chrosomus eos*
Record: Hanek et al. 1975 (Ont)

38 **Hamuli 36–38 long** .... ***D. cheloideus* Rogers, 1967 (Fig. 26:13, Table 17)**
On gills of *Rhinichthys atratulus*
Records: Hanek and Fernando 1972b (Ont); Hanek et al. 1975 (Ont)

Hamuli 29–34 long .... ***D. richardsonius* Monaco and Mizelle, 1955 (Fig. 26:34, Table 17)**
On gills of *Richardsonius balteatus*
Record: Monaco and Mizelle 1955 (BC)

Records of unidentified *Dactylogyrus* spp. are listed from:

Catostomus commersoni — Molnar et al. 1974, Ontario; *Cottus bairdi* — Dechtiar 1972b, 1972c, Ontario, Lubinsky and Loch 1979, Manitoba; *Gasterosteus aculeatus* — Lester 1974, British Columbia; *Hybognathus hankinsoni* — Molnar et al. 1974, Ontario; *Moxostoma erythrurum, M. macrolepidotum* — Dechtiar 1972b, Ontario; *Nocomis biguttatus* — Molnar et al. 1974, Ontario; *Notropis atherinoides, N. cornutus* — Dechtiar 1972b, Ontario; *N. heterolepis* — Molnar et al. 1974, Ontario, Cone 1980, New Brunswick; *N. hudsonius* — Dechtiar 1972b, 1972c, Ontario, Lubinsky and Loch 1979, Manitoba; *Pimephales promelas* — Dechtiar 1972c, Ontario, Lubinsky and Loch 1979, Manitoba; *Semotilus atromaculatus* — Molnar et al. 1974, Ontario, Cone 1980, New Brunswick; *S. margarita* — Cone 1980, New Brunswick.

Pellucidhaptor Price and Mizelle, 1964 (Fig. 27:0)

Dactylogyridae: body elongate, cuticle thin; two pairs of eyes. Haptor separated from body by distinct peduncle, with one pair of obvious, dorsal hamuli associated with dorsal transverse bar; ventral hamuli vestigial,[49] ventral transverse bar lacking; 14 marginal hooks. Vas deferens (when observed) looping left intestinal caecum;[50] penis tubular, surrounded proximally by accessory piece. Ovary equatorial, vagina (where observed) dextroventral; vitellaria, coextensive with intestinal caeca, may extend to haptor. On body surface and gills and in nasal cavities of North American (and Eurasian) freshwater fishes (Cypriniformes).

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[49] Price and Mizelle (1964) proposed *Pellucidhaptor* with the type species, *P. pellucidhaptor* (="*Dactylogyrus*" sp. of Mizelle and Price, 1963), described as having an extra pair (4A) of marginal hooks, which Kearn (1968) regarded as vestigial ventral hamuli — see footnote 43.

[50] Described by Kritsky et al. (1972) for *P. micracanthus*.

27:0

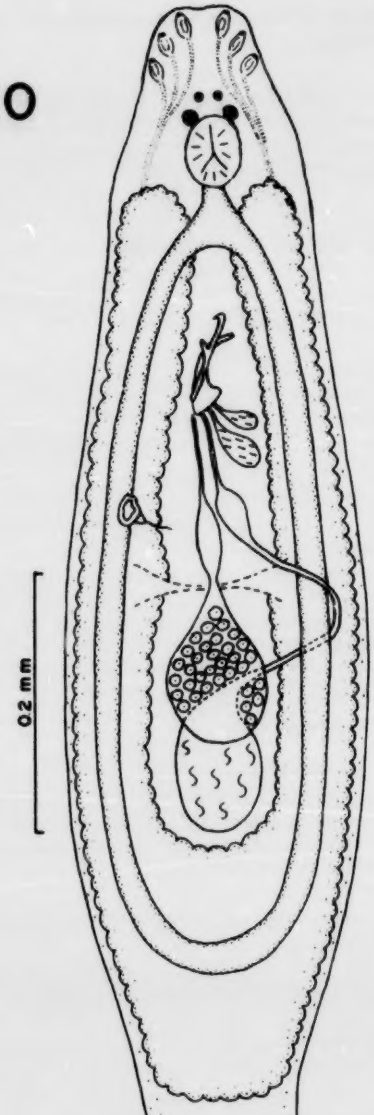

FIG. 27:0. *Pellucidhaptor* — generic characters (based on Chien and Rogers 1970 with original observations): whole animal, ventral view.

Key to species of *Pellucidhaptor*

1 Hamuli more than 100 long. Parasites of catostomids 2

Hamuli less than 100 long. Parasites of cyprinids .... *P. pellucidhaptor* Price and Mizelle, 1964 (Fig. 27:3)

Morphometric data (from Price and Mizelle 1964): body 1056 (787–1341) by 184 (133–198); hamuli 78 (69–89) long; transverse bar 57 (49–62) transverse length; marginal hooks 16–22; penis 50 (47–56); accessory piece 39 (38–42).

Records: Anon. 1978 (BC); Arai and Mudry 1983 (BC)

Remarks: Anon. (1978) erroneously gave the distribution of this species as Lake Erie, citing Dechtiar (1972b). However, the only records listed by Dechtiar (1972b) are for *Pellucidhaptor* spp. (see below).

2 Hamuli more than 200 long; bar more than 100 transverse length .... *P. catostomi* Dechtiar, 1969 (Fig. 27:1)

Morphometric data (from Dechtiar 1969): body 1104 (600–1886) by 276 (160–292); hamuli 244 (208–270) long; transverse bar 123 (105–156) transverse length by 51 (32–64) median width; marginal hooks 23 (21–25); penis 92 (85–109); accessory piece 84 (79–95).

In nasal cavities of *Catostomus catostomus*
Record: Dechtiar 1969 (Ont)

Hamuli less than 200 long; bar less than 100 transverse length .... *P. nasalis* Dechtiar, 1969 (Fig. 27:2)

Morphometric data (from Dechtiar 1969): body 731 (566–900) by 178 (109–260); hamuli 142 (111–182) long; transverse bar 75 (68–96) transverse length by 38 (32–45) median width; marginal hooks 21 (17–23) long; penis 68 (51–106); accessory piece 51 (36–85).

In nasal cavities of *Catostomus catostomus* (5); *C. commersoni* (1,2,3,4)
Records: 1. Dechtiar 1969 (Ont); 2. 1972c (Ont); 3. Lubinsky and Loch 1979 (Man); 4. Cone 1980 (NB); 5. Anon. 1981 (BC)

Records of unidentified *Pellucidhaptor* spp. are listed from:

Carpiodes cyprinus, Moxostoma macrolepidotum — Dechtiar 1972b, Ontario.

Pseudacolpenteron Bykhovsky and Gusev, 1955 (Fig. 28:0)

Dactylogyridae: body robust, cuticle thin. Head organs and eyespots present. Haptor trapezoidal in shape with 14 marginal hooks; hamuli and bar(s) lacking. Penis curved, sclerotized, tubular; accessory piece thin, plate-like, partly enfolding penis. Vagina present. Vitellaria fill all available space between pharynx and haptor. On body surface of North American (and Eurasian) freshwater fishes (Cypriniformes). One species on Canadian fishes.

Pseudacolpenteron pavlovskii Bykhovsky and Gusev, 1955 (Fig. 28:1)

Morphometric data (from Bykhovsky and Gusev 1955): body 450–670 by 160–220; marginal hooks 23–37; penis curved part 47–52, penis straight part 38–43; accessory piece 33–38. (Dechtiar (1971) gave the length of specimens found on carp in Ontario as 556–829.)

On fins and body surface of *Cyprinus carpio*
Records: Dechtiar 1971 (Ont); 1972b (Ont)

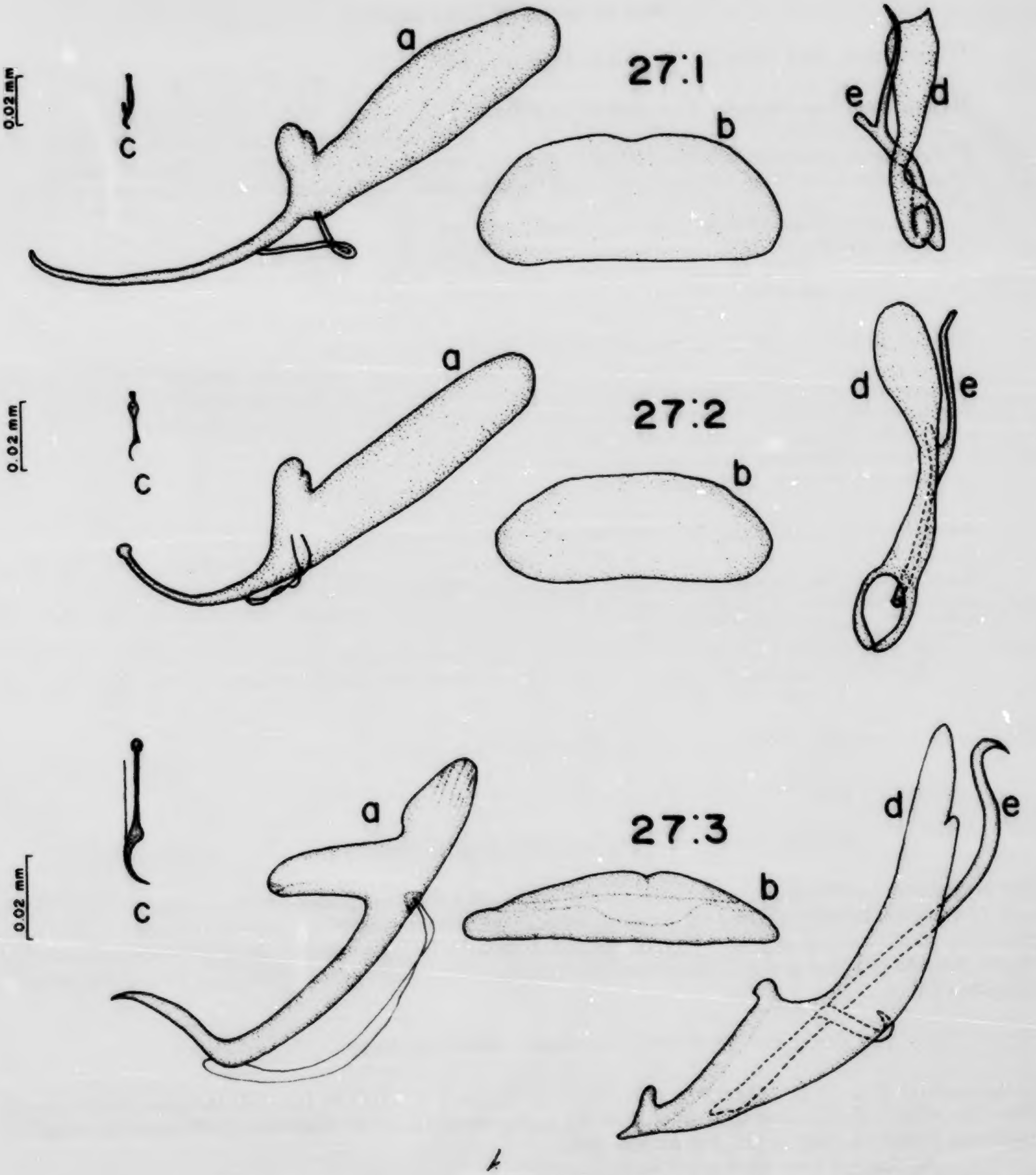
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FIG. 27:1–27:3. ***Pellucidhaptor*** **spp. 27:1.** ***P. catostomi*** **(redrawn from Dechtiar 1969): a. hamulus; b. transverse bar; c. marginal hook; d. penis; e. accessory piece. 27:2.** ***P. nasalis*** **(redrawn from Dechtiar 1969): a. hamulus; b. transverse bar; c. marginal hook; d. penis; e. accessory piece. 27:3.** ***P. pellucidhaptor*** **(redrawn from Price and Mizelle 1964): a. hamulus; b. transverse bar; c. marginal hook; d. penis; e. accessory piece.**

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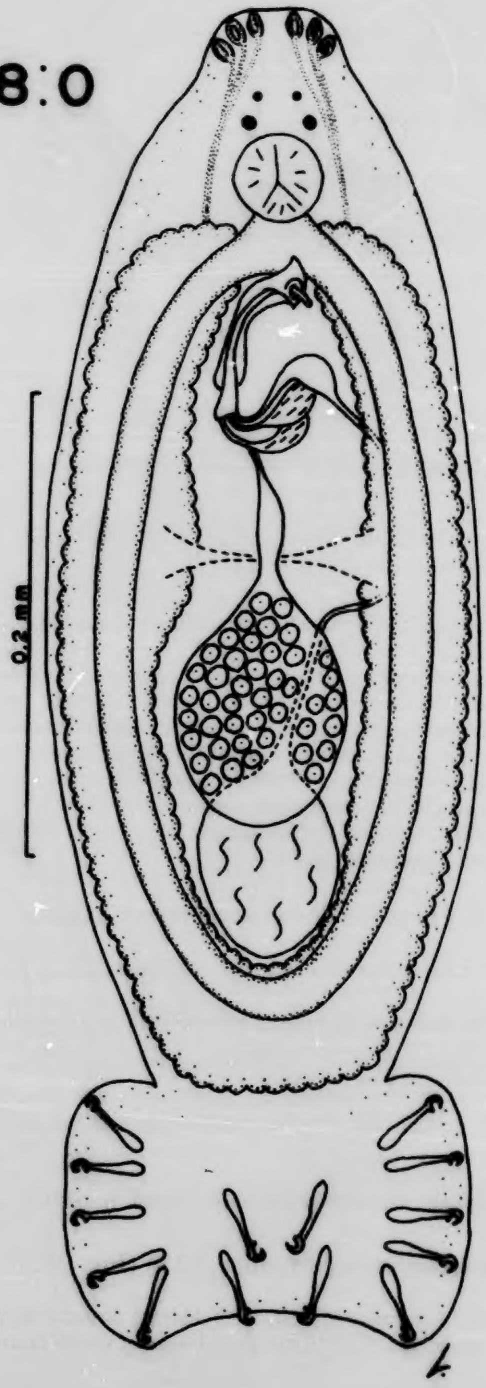

FIG. 28:0. *Pseudacolpenteron* — generic characters (based on Bykhovsky and Gusev 1955): whole animal, ventral view.

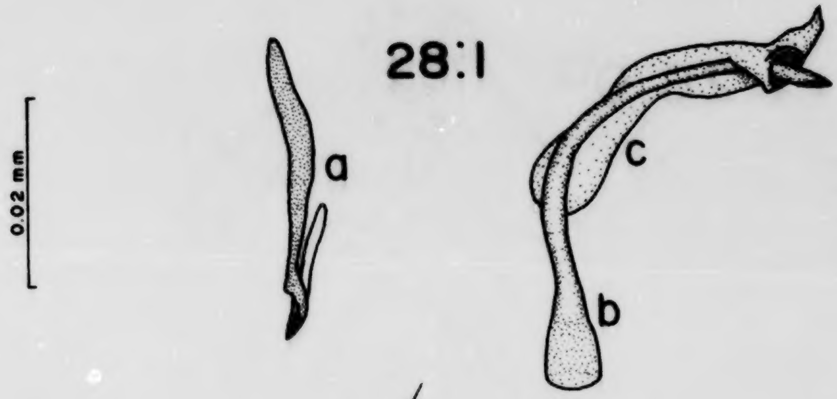

FIG. 28:1. *Pseudacolpenteron pavlovskii* (modified from Bykhovsky and Gusev 1955): a. marginal hook; b. penis; c. accessory piece.

PSEUDOMURRAYTREMATIDAE[51] (Kritsky, Mizelle and Bilqees, 1978, subfam.) status emend.

Dactylogyrida: body small or medium in size, anterior extremity with cephalic lobes or lappets; head organs present or absent; cephalic glands in two groups in anterolateral region of body. Two pairs of eyes. Haptor, more or less distinct, with 14 marginal hooks of which 12 are peripheral and two central; two pairs hamuli (one dorsal and one ventral) supported by two or three bars, present or (secondarily) absent. Mouth ventral, pharynx present, muscular; intestinal caeca confluent or not. Testis intercaecal, postovarian; vas deferens looping dorsoventrally round left intestinal caecum; seminal vesicle enclosed in ejaculatory bulb; penis sclerotized, U-shaped with distal flange; accessory piece multiramous, sclerotized, attached to proximal region of penis. Ovary looping right intestinal caecum; vagina opening on right side of body, submarginal, comprising a distal, sclerotized funnel and proximal, coiled duct. Vitellaria coextensive with intestinal caeca or extending to level of haptor. Freshwater, on Cypriniformes.

Key to genera of Pseudomurraytrematidae

1 Haptor without hamuli or bars; intestinal caeca not confluent 2

Haptor with two pairs of hamuli and three (one ventral and two dorsal) transverse bars .... *Pseudomurraytrema*

2 Cephalic region with large, semicircular lappets; haptor disc-like, slightly muscular .... *Anonchohaptor*

Cephalic region lacking cephalic lappets; haptor cup-shaped, muscular .... *Icelanonchohaptor*

Anonchohaptor Mueller, 1938 (Fig. 29:0)

Pseudomurraytrematidae: anterior extremity of body with distinct cephalic lappets; head organs present or absent. Haptor disc-like, slightly muscular, with 14 marginal hooks of which 12 are peripheral and two central;

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[51] The Pseudomurraytrematinae of Kritsky et al. (1978a) is elevated to family status, of equivalent rank to the Ancyrocephalidae and Dactylogyridae.

29:0

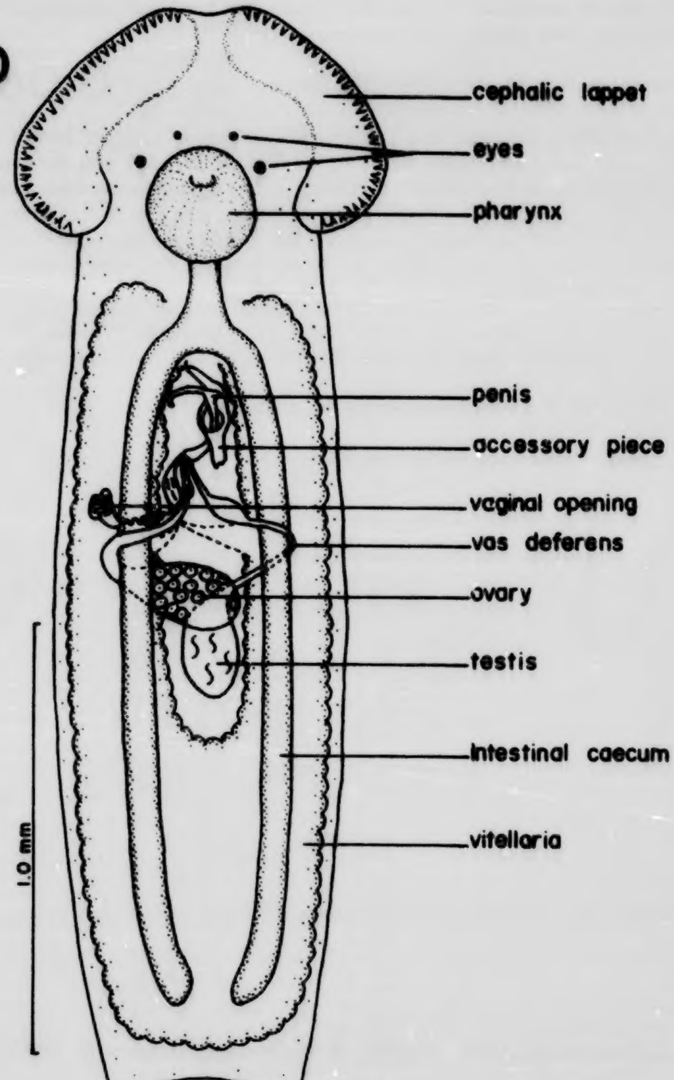
cephalic lappet
eyes
pharynx
penis
accessory piece
vaginal opening
vas deferens
ovary
testis
intestinal caecum
vitellaria
1.0 mm
haptor
marginal hook

FIG. 29:0. *Anonchohaptor* — generic characters (based on Mueller 1938 and Dechtiar and Dillon 1974): whole animal, ventral view.

hamuli and bars absent. Intestinal caeca ending blindly, not confluent. On gills of North American freshwater fishes (Catostomidae). One species on Canadian fishes.

Anonchohaptor anomalum Mueller, 1938 (Fig. 29:1)

Morphometric data (from Dechtiar and Dillion 1974) based on material from *Catostomus catostomus* and *C. commersoni*: body 3.12 (1.89–4.00) mm long by 0.61 (0.38–1.81) mm wide; cephalic lappets prominent; pharynx 341 (246–556) transverse diameter. Haptor with 12 marginal and two central hooks of similar shape and size, 17 (15–21) long. Penis 48 (39–56) long; accessory piece with two arms, 54 (45–63) long.

On gills and fins of *Carpiodes cyprinus* (1,2,8); *Catostomus catostomus* (3,4,5,7,9,10); *C. commersoni* (1,2,3,4,6,7,8,10); *C. macrocheilus* (7,10); *Moxostoma anisurum* (1,2,8); *M. erythrurum* (1,2,8); *M. macrolepidotum* (1)

Records: 1. Dechtiar 1972b (Ont); 2. 1972c (Ont); 3. Dechtiar and Dillon 1974 (Ont); 4. Threlfall 1974 (Lab); 5. Arthur et al. 1976 (YT); 6. Cone 1980 (NB); 7. Anon. 1978 (BC); 8. Lubinsky and Loch 1979 (Man); 9. Anon. 1981 (BC); 10. Arai and Mudry 1983 (BC)

Record of an unidentified *Anonchohaptor* sp. is listed from:

Carpiodes cyprinus — Dechtiar 1972b, Ontario.

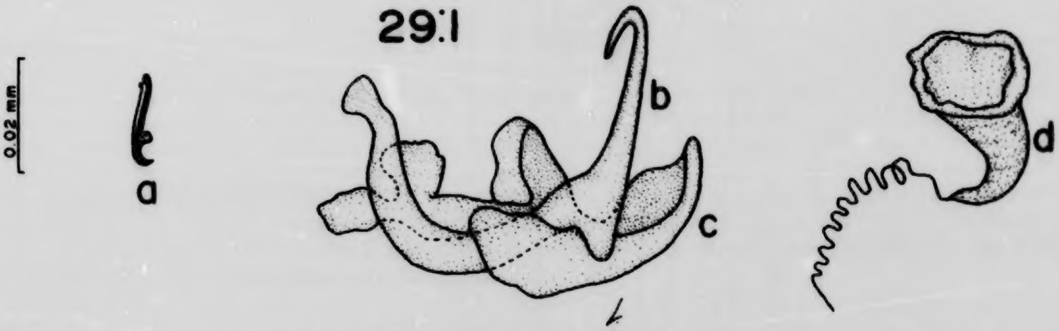

FIG. 29:1. *Anonchohaptor anomalum* (redrawn from Dechtiar and Dillon 1974): a. marginal hook; b. penis; c. accessory piece; d. vagina.

Icelanonchohaptor Leiby, Kritsky and Peterson, 1972 (Fig. 30:0)

Pseudomurraytrematidae: anterior extremity of body with poorly developed cephalic lappets; head organs present. Haptor cup-shaped, muscular, with 14 marginal hooks of which 12 are peripheral and two central; hamuli and bars absent. Intestinal caeca ending blindly, not confluent. On gills of North American freshwater fishes (Catostomidae). One species on Canadian fishes.

Icelanonchohaptor fyviei Dechtiar and Dillon, 1974 (Fig. 30:1)

Morphometric data (from Dechtiar and Dillon 1974): body 993 (768–1198) long by 264 (189–368) wide; pharynx 117 (80–156) in transverse diameter. Haptor cup-like, 171 (103–249) in diameter with 12 marginal hooks, 14–17 long, and two central hooks, 22–25 long, of similar shape. Penis 32 (26–40) long; accessory piece with two arms 32 (27–38) long.

On gills of *Carpiodes cyprinus*

Record: Dechtiar and Dillon 1974 (Ont)

30:0

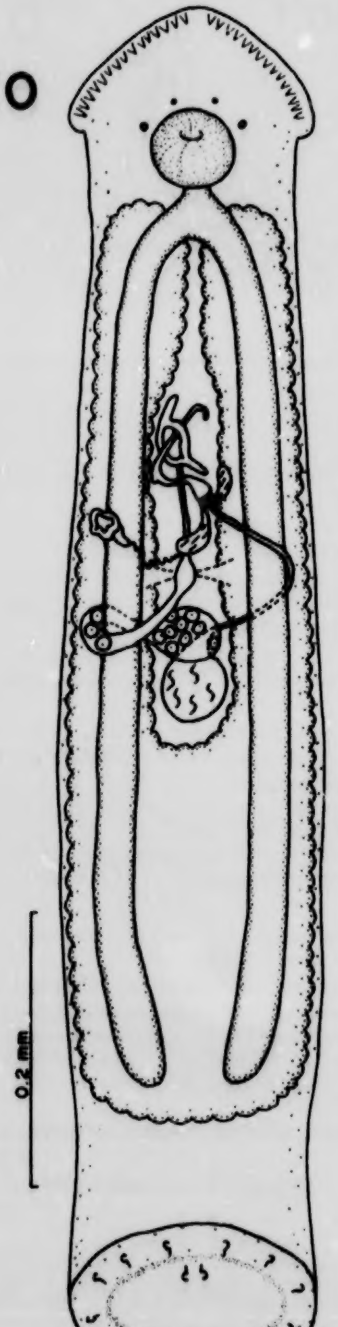

FIG. 30:0. *Icelanonchohaptor* — generic characters (redrawn from Leiby et al. 1972): whole animal, ventral view.

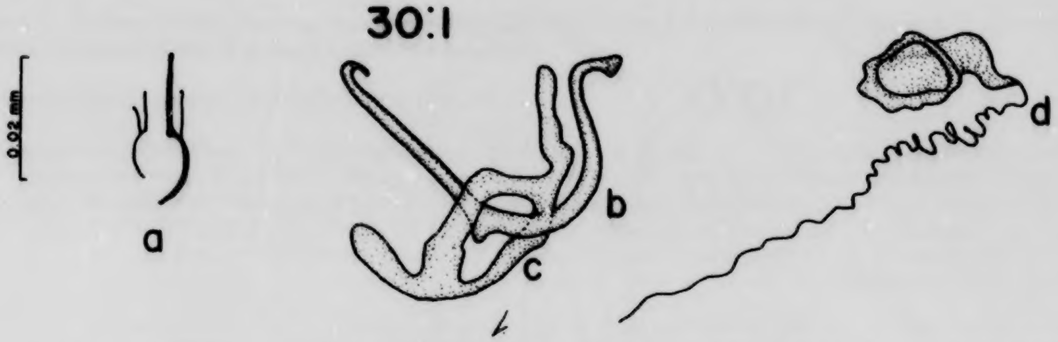

FIG. 30:1. *Icelanonchohaptor fyviei* (redrawn from Dechtiar and Dillon 1974): a. marginal hooks; b. penis; c. accessory piece; d. vagina.

Pseudomurraytrema Bykhovsky, 1957 (Fig. 31:0)

Pseudomurraytrematidae: body elongate, anterior extremity with poorly developed cephalic lobes, head organs present or absent. Haptor separated from body by peduncle; two pairs of hamuli (one dorsal, one ventral); median, ventral transverse bar and two submedian, dorsal bars, none articulating with each other; 14 marginal hooks of which 12 are peripheral and two central. Intestinal caeca confluent posteriorly. On gills of North American freshwater fishes (Catostomidae).

Key to species of *Pseudomurraytrema*

1 Ventral bar distinctly bowed posteriorly; dorsal bars inflated medianly; hamuli more or less equal in size .... *P. alabarrum* Rogers, 1966 (Fig. 31:1, Table 19)

Syn: *P. muelleri* Price, 1967 (new syn.)
On gills of *Catostomus commersoni*
Record: Price and Arai 1967 (Alta)
Remarks: Margolis and Arthur (1979) listed this species as *P. muelleri* and noted the possibility of the above synonymy which was confirmed by Rogers (pers. comm.).

Ventral bar straight, or bowed anteriorly; dorsal bars narrow, with median hook; hamuli unequal in size, dorsal hamuli longer with elongate shaft .... *P. copulatum* (Mueller, 1938) Bykhovsky, 1957 (Fig. 31:2, Table 19)

On gills of *Catostomus catostomus* (3,5,6); *C. commersoni* (1,2,3,4,6); *C. macrocheilus* (3,5,6); *Moxostoma anisurum* (1,2,4); *M. erythrurum* (1); *M. macrolepidotum* (1)
Records: 1. Dechtiar 1972b (Ont); 2. 1972c (Ont); 3. Anon. 1978 (BC); 4. Lubinsky and Loch 1979 (Man); 5. Anon. 1981 (BC); 6. Arai and Mudry 1983 (BC)

Records of undescribed[52] or unidentified species of *Pseudomurraytrema* are listed from:

Moxostoma anisurum, M. erythrurum — Dechtiar 1972c, Ontario, Lubinsky and Loch 1979, Manitoba; *M. macrolepidotum* — Dechtiar 1972b, Ontario.

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[52] The record for *M. macrolepidotum* was listed by Dechtiar (1972b) as *P. moxostomi*. As Margolis and Arthur (1979) pointed out, this is a *nomen nudum* as the species has not been described.

31:0

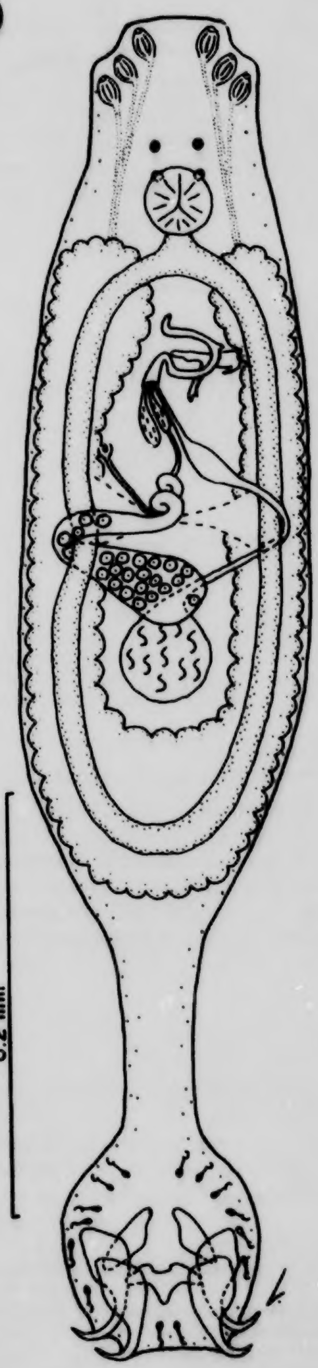

FIG. 31:0. *Pseudomurraytrema* — generic characters (based on Chien 1969 with original observations): whole animal, ventral view.

Table 19. Comparative measurements (in μm) of the species of *Pseudomurraytrema* Bykhovsky, 1957, recorded from fishes of Canada.

Species	*P. alabarrum*	*P. copulatum*
Source of data	Rogers (1966)	Kritsky and Hathaway (1969)
Body: length	1360 (1070–1700)	495 (399–597)[b]
width	184 (150–220)	97 (81–128)
Dorsal hamuli: length	74 (64–85)	60 (58–64)
Dorsal bars: transverse length	73 (65–80)	39 (37–40)
width	17 (14–20)	—
Ventral hamuli: length	75 (64–82)	48 (44–50)
Ventral bar: transverse length	69 (62–80)	48 (44–52)
Marginal hooks: total length	14 "constant"	13 (12–14)
Penis: length	38 (37–40)	37 (35–38)
Accessory piece: length	29 (27–30)[a]	38 (30–45)
Site	gills	gills
Host(s)	*Catostomus commersoni*	*Catostomus catostomus* *C. commersoni* *C. macrocheilus* *Moxostoma anisurum* *M. erythrurum* *M. macrolepidotum*
Locality(ies)	Alberta	British Columbia Ontario

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[a] Measurement of middle arm (Rogers 1966).

[b] Measurements provided by Mueller (1938) and Mizelle and Klucka (1953) were larger.

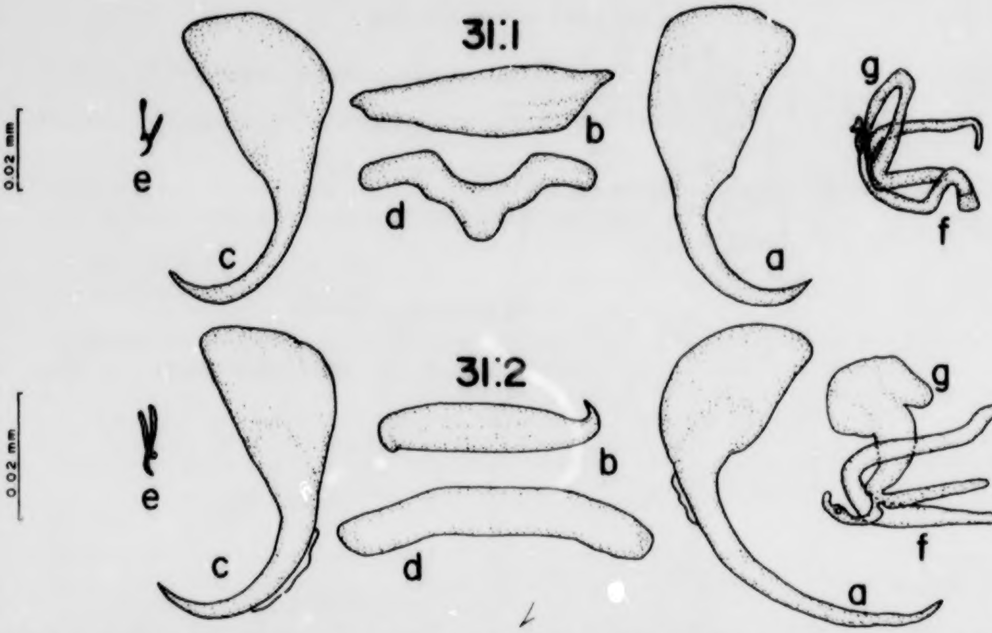

FIG 31:1-31:2. *Pseudomurraytrema* spp. 31:1. *P. alabarrum* (redrawn from Rogers 1966): a. dorsal hamulus; b. dorsal bar of right hamulus (lateral extremity on left); c. ventral hamulus; d. ventral bar; e. marginal hook; f. penis; g. accessory piece. 31:2. *P. copulatum* (redrawn from Kritsky and Hathaway 1969 with original observations): a. dorsal hamulus; b. dorsal bar of right hamulus (lateral extremity on left); c. ventral hamulus; d. ventral bar; e. marginal hook; f. penis; g. accessory piece.

TETRAONCHIDAE Bykhovsky, 1937

Dactylogyrida: body elongate; haptor discrete but small carrying 16 marginal hooks;[53] two pairs of hamuli (one dorsal and one ventral) and a single transverse bar. Pharynx present, muscular, leading to single intestinal caecum. Testis single; penis with accessory piece; genital pore postpharyngeal, median, or submedian. Ovary entire, pretesticular; vitellaria coextensive with intestinal caecum. Freshwater, on Salmoniformes. The family contains one genus, *Tetraonchus*.[54]

Tetraonchus Diesing, 1850 (Fig. 32:0)

Tetraonchidae: haptor with or without additional sclerotized plates (rudimentary remains of a second transverse bar or "fan-shaped plates" of Soviet authors, see Dechtiar 1972a); transverse bar variable in shape. Penis tubular, sclerotized, encircled distally by accessory piece. Vagina not observed. On gills of North American and Eurasian Esocidae and Salmonidae.

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[53] See Llewellyn (1970) for comment on the position of pair I which may prove to be central on the oncomiracidial haptor and be displaced, during postlarval development, by the hamuli and connecting bar.

[54] Spassky and Roytman (1958) proposed the genus *Salmonchus* to accommodate tetraonchids parasitizing salmonids and retained *Tetraonchus* for species found on esocids and "thymallids". Strelkov (1963) recombined the species into a single genus, designating two subgenera: *Tetraonchus* (*Tetraonchus*) and *Tetraonchus* (*Salmonchus*). Dechtiar (1972a) reviewed the systematics of the group, discussed the importance of the "fan-shaped/flabellate bars" as taxonomic characters and concluded there was no reliable basis for subdividing the genus *Tetraonchus*. Thus, *Tetraonchus* is regarded by the present author as the only genus within the Tetraonchidae (as defined above) and the generic diagnosis is close to that of the family.

32:0

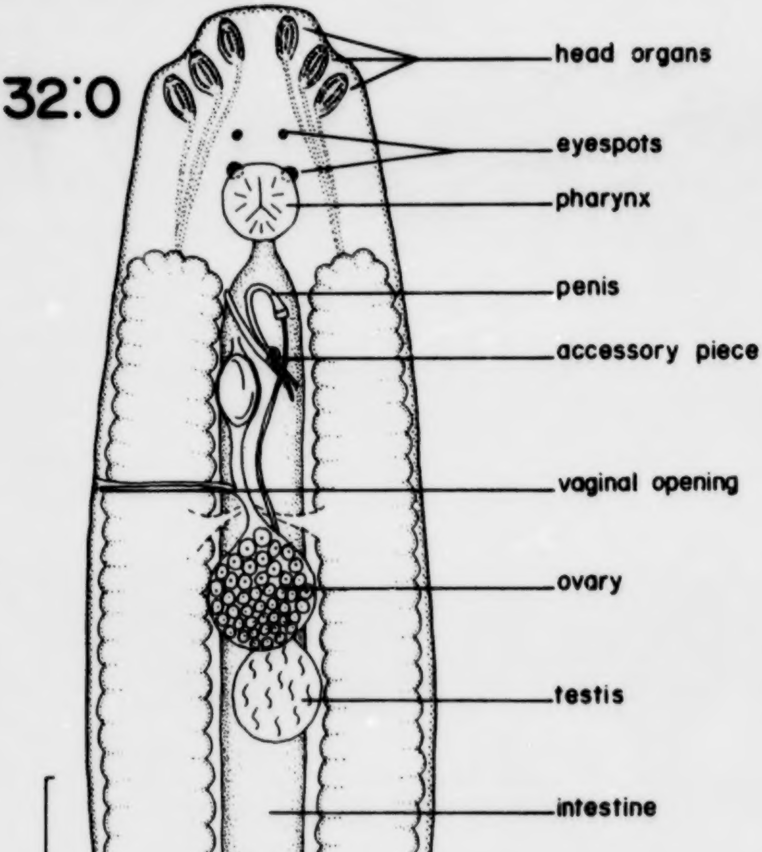
head organs
eyespots
pharynx
penis
accessory piece
vaginal opening
ovary
testis
intestine
vitellaria
0.5 mm
marginal hook
haptor
hamuli
transverse bar

FIG. 32:0. *Tetraonchus* — generic characters (based on Bykhovsky 1957): whole animal, ventral view.

Key to species of *Tetraonchus*

1 Parasites of Esocidae 2

Parasites of Salmonidae (Salmoninae, Coregoninae, and Thymallinae) 3

2 Transverse bar (butterfly-shaped) 27–35 transverse length; dorsal hamuli with prominent deep root, ventral hamuli with prominent superficial root. Penis 51–56 long .... *T. loftusi* Dechtiar, 1972 (Fig. 32:3, Table 20)

On gills of *Esox masquinongy*
Record: Dechtiar 1972a (Ont)

Transverse bar (butterfly-shaped) 69–72 transverse length; dorsal hamuli with less prominent deep root, ventral hamuli with less prominent superficial root. Penis 78–81 long .... *T. monenteron* (Wagener, 1857) Diesing, 1858 (Fig. 32:4, Table 20)

On gills of *Esox lucius* (1,2,3,4,5,6,7,8,9,10); *Salvelinus namaycush*[55] (9)
Records: 1. Threlfall and Hanek 1970a (Lab); 2. Hanek and Fernando 1972a (Ont); 3. Dechtiar 1972a (Ont); 4. 1972b (Ont); 5. 1972c (Ont); 6. Arai and Chien 1973 (Alta); 7. Arthur et al. 1976 (YT); 8. Watson 1977 (Man); 9. Chinniah and Threlfall 1978 (Lab); 10. Lubinsky and Loch 1979 (Man)

3 Dorsal and ventral hamuli with slender, V-shaped deep root; transverse bar butterfly-shaped. Penis 91–117 long .... *T. borealis* (Olsson, 1893) Monticelli, 1905 (Fig. 32:2, Table 20)

On gills of *Thymallus arcticus*
Records: Wobeser et al. 1976 (Sask); Arthur et al. 1976 (YT); Anon. 1978 (BC); Arai and Mudry 1983 (BC)

Dorsal and ventral hamuli with broad, wedge-shaped deep root; transverse bar not butterfly-shaped. Penis not more than 80 long 4

4 Transverse bar slender, posterior margin not indented, 16–63 transverse length. Penis 41–63 long .... *T. variabilis* Mizelle and Webb, 1953 (Fig. 32:5, Table 20)

On gills[56] of *Prosopium coulteri* (5); *P. cylindraceum* (1,2,4); *P. williamsoni* (6,7,8); *Salvelinus fontinalis* (2); unspecified Salmonidae (3)
Records: 1. Dechtiar 1972a (Ont); 2. Hicks and Threlfall 1973 (Lab); 3. Collins and Dechtiar 1974 (Ont); 4. Arthur et al. 1976 (YT); 5. Mudry and Anderson 1977 (BC); 6. Anon. 1978 (BC); 7. Anon. 1981 (BC); 8. Arai and Mudry 1983 (BC)

Transverse bar robust, posterior margin indented, 20–25 transverse length. Penis 80 long .... *T. alaskensis* Price, 1937 (Fig. 32:1, Table 20)

On gills of *Oncorhynchus kisutch* (4); *Salvelinus alpinus* (1,2); *S. malma* (1,3,4,5)
Records: 1. Mudry and McCart 1976 (YT); 2. Beverley-Burton 1978 (NWT); 3. Anon. 1978 (BC); 4. Anon. 1981 (BC); 5. Arai and Mudry 1983 (BC)

ORDER GYRODACTYLIDA[57] Bykhovsky, 1937

Haptor entire: marginal hooks 16 with the posteriormost pair (I) not migrating anteriorly but remaining peripheral. One pair hamuli usually present, ventrally projecting, supported by one, or two, transverse bars. Mouth lacking both oral or buccal suckers. Viviparous. The order contains one family, Gyrodactylidae.

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[55] Chinniah and Threlfall (1978) considered this record to be "probably accidental". *Tetraonchus* spp. show a high degree of host specificity and *T. monenteron* typically parasitizes pike.

[56] Anon. (1981) found *T. variabilis* in the ureter of one *P. williamsoni*.

[57] Gyrodactylidea of Bykhovsky (1937).

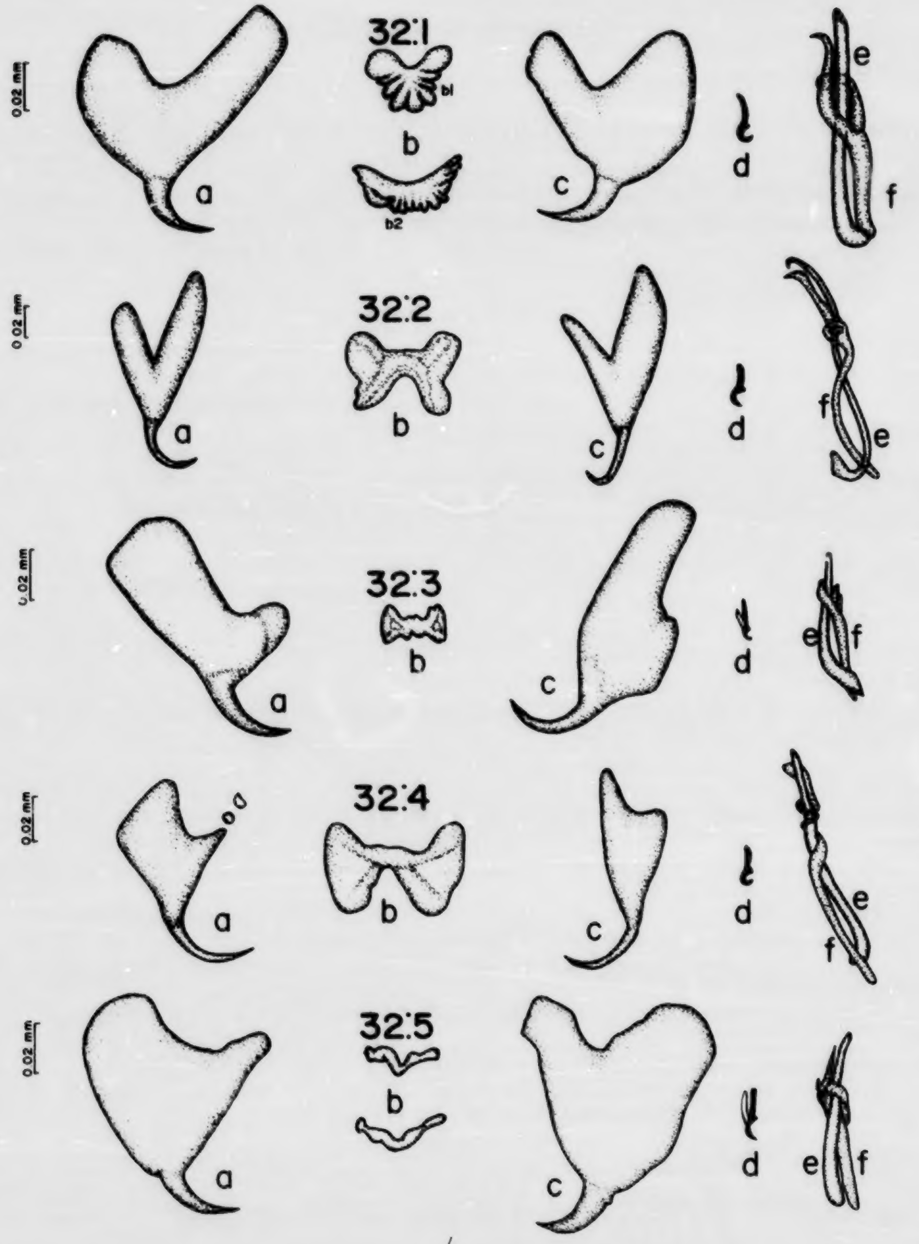

FIG. 32:1–32:5. *Tetraonchus* spp. 32:1. *T. alaskensis* (a–f modified from Price 1937, b2 from Bykhovskaya-Pavlovskaya et al. 1962): a. dorsal hamulus; b1,b2 transverse bar (morphological variations); c. ventral hamulus; d. marginal hook; e. penis; f. accessory piece. 32:2. *T. borealis* (modified from Spassky and Roytman 1958): a. dorsal hamulus; b. transverse bar; c. ventral hamulus; d. marginal hook; e. penis; f. accessory piece. 32:3. *T. loftusi* (redrawn from Dechtiar 1972a): a. dorsal hamulus; b. transverse bar; c. ventral hamulus; d. marginal hook; e. penis; f. accessory piece. 32:4. *T. monenteron* (modified from Bykhovskaya-Pavlovskaya et al. 1962): a. dorsal hamulus; b. transverse bar; c. ventral hamulus; d. marginal hook; e. penis; f. accessory piece. 32:5. *T. variabilis* (modified from Mizelle and Webb 1953): a. dorsal hamulus; b. transverse bar (morphological variations); c. ventral hamulus; d. marginal hook; e. penis; f. accessory piece.

TABLE 20. Comparative measurements (in mm, unless otherwise noted) of the species of *Tetraonchus* Diesing, 1858, recorded from fishes of Canada.

Species	*T. alaskensis*	*T. borealis*	*T. loftusi*	*T. monenteron*	*T. variabilis*
Source of data	Price (1937)	Arthur et al. (1976)	Dechtiar (1972a)	Bykhovskaya-Pavlovskaya et al. (1962)	Mizelle and Webb (1953)
Body: length	2.0	1.01–1.78	1.70–2.36	1.17	1.1–2.3
width	0.67–0.72	0.20–0.50	0.33–0.51	up to 0.02	0.13–0.56
Haptor: width	0.23–0.28	—	0.15–0.21	—	0.14–0.26
Dorsal hamuli: length	110[a]	82–107[a]	91–103[a]	69–72[a]	76–105[a]
Ventral hamuli: length	107[a]	93–120[a]	102–107[a]	95–106[a]	76–135[a]
Ventral bar: transverse length	20–25[a]	68–105[a]	27–35[a]	69–72[a]	16–63[a]
width	30–35[a]	—	—	9–10[a]	"variable"
Penis: length	80[a]	91–117[a]	51–56[a]	78–81[a]	41–63[a]
Accessory piece: length	60–65[a]	86–118[a]	—	59–87[a]	36–58[a]
Site	gills	gills	gills	gills	gills
Host(s)	*Oncorhynchus kisutch* *Salvelinus alpinus* *S. malma*	*Thymallus arcticus*	*Esox masquinongy*	*Esox lucius* *Salvelinus namaycush*[b]	*Prosopium coulteri* *P. cylindraceum* *P. williamsoni* *Salvelinus fontinalis*
Locality(ies)	British Columbia Northwest Territories Yukon Territory	British Columbia Saskatchewan Yukon Territory	Ontario	Alberta Labrador Manitoba Newfoundland Ontario Yukon Territory	British Columbia Labrador Ontario Yukon Territory

[a] Measurements in µm.
[b] See footnote 55 on p. 115.

33:0

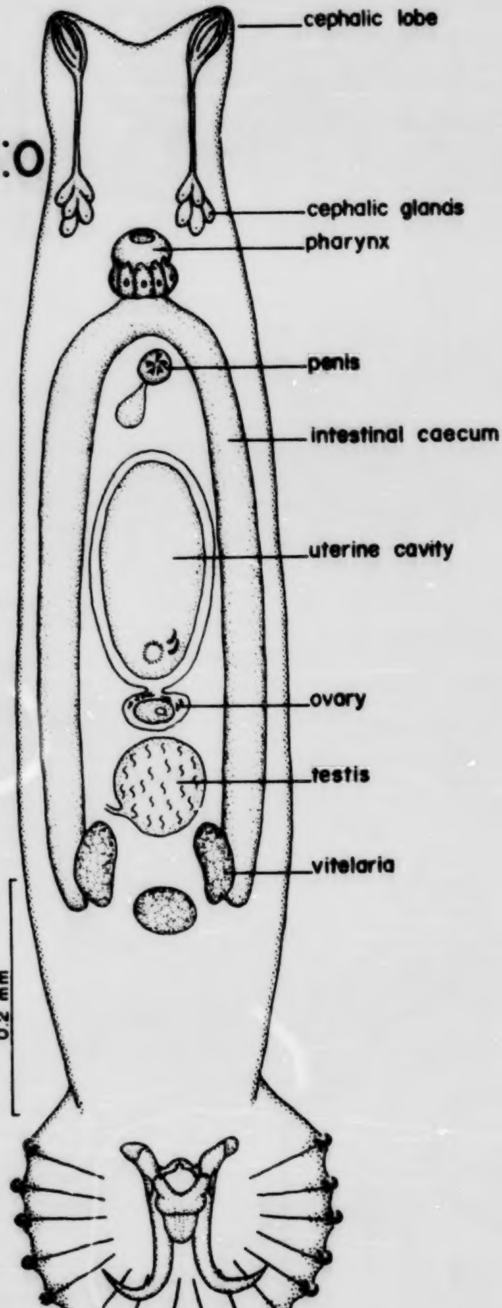
cephalic lobe
cephalic glands
pharynx
penis
intestinal caecum
uterine cavity
ovary
testis
vitelaria
0.2 mm

FIG. 33:0. Generalized gyrodactylid — family characters based on *Gyrodactylus* (modified from Malmberg 1970): whole animal, ventral view.

GYRODACTYLIDAE Cobbold, 1864 (Fig. 33:0)

Gyrodactylida: body small with two cephalic lobes. Eyes absent. Intestinal caeca not confluent posteriorly. Testis median; penis, muscular bulb armed with row of spines. Ovary median, immediately posterior to uterine cavity; vagina absent. Genital pore median or submedian, posterior to pharynx. Marine, freshwater, and brackish water, on teleosts.

Key to genera of Gyrodactylidae

1 Marginal hooks evenly distributed on haptor; each hamulus, with single (superficial) root; two (one dorsal and one ventral) transverse bars (Fig. 33:0, 34:0) 2

Marginal hooks not evenly distributed on haptor but in three groups (two lateral and one posterior); each hamulus with two roots (deep and superficial); one (ventral) transverse bar (Fig. 35:0). On marine teleosts 3

2 Peduncle surrounded by anteriorly directed flange[58] armed with sclerotized points. On Cyprinodontidae (*Fundulus* spp.) .... *Fundulotrema*

Peduncle lacking anteriorly directed flange. On freshwater, brackish water, or marine teleosts .... *Gyrodactylus*

3 Haptor umbrella-shaped, ventrally directed, wider than body; marginal hooks distinctly flexed, radiating from central, dorsal area of haptor; suction disc, supported by sclerotized bars, projecting from ventral surface of haptor .... *Gyrodactyloides*

Haptor cup-shaped, posteriorly directed, not wider than body; marginal hooks not flexed, oriented anteroposteriorly; suction disc absent; hamuli and anterolateral marginal hooks supported by sclerotized plate .... *Laminiscus*

Fundulotrema Kritsky and Thatcher, 1977 (Fig. 34:0)

Gyrodactylidae: body elongate, with distinct peduncle, surrounded by anteriorly directed flange armed with sclerotized points. Marginal hooks distributed evenly on periphery of haptor. Hamuli with elongate superficial root; ventral bar with pronounced anterolateral processes and elongate, rectangular shield; dorsal bar butterfly-shaped. On body surface of North American teleosts (Cyprinodontidae[59]). One species on Canadian fishes.

Fundulotrema prolongis (Hargis, 1955) Kritsky and Thatcher, 1977

Morphometric data (from Hanek and Fernando 1971b): body 600–696 long, 84–96 wide; hamuli 71–76, root 36–39, shaft 41–43, point 23–25; dorsal bar length 14–18, width (median) 1–2; ventral bar length 23–25, width (median) 7–8, anterolateral process length 13; marginal hooks, total length 47–48, sickle 6–7.

Syn: *Gyrodactylus prolongis* Hargis, 1955
On fins of *Fundulus diaphanus* (1); *F. heteroclitus* (2)
Records: 1. Hanek and Fernando 1971b (Ont); 2. Dickinson and Threlfall 1975 (Nfld)

Gyrodactyloides Bykhovsky, 1947 (Fig. 35:0)

Gyrodactylidae: body elongate. Marginal hooks, with elongate shaft more or less distinctly flexed near middle, distributed in three groups on periphery of haptor: two anterolateral with four hooks each and one

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[58] Peduncular bar of Kritsky and Thatcher (1977).

[59] Primarily freshwater but can move into brackish water and marine situations.

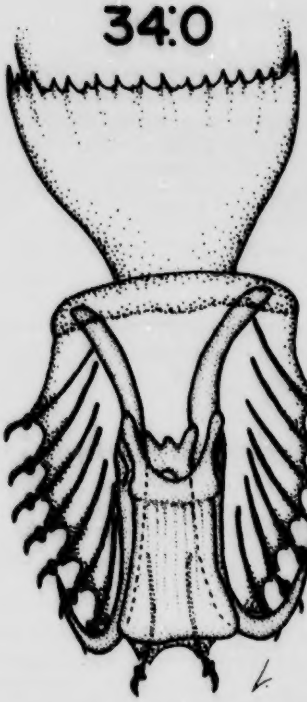

FIG. 34:0. *Fundulotrema* — haptoral characters (based on Hargis 1955, with original observations).

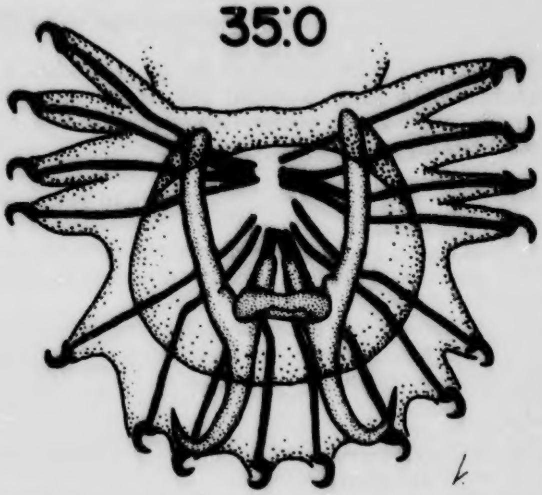

FIG. 35:0. *Gyrodactyloides* — haptoral characters (based on Pálsson and Beverley-Burton 1983).

posterior with eight. Hamuli with short deep root and elongate, forwardly directed, superficial root. One connecting transverse bar present. Haptor with ventrally projecting suction disc supported by complex, sclerotized structure connecting with superficial roots of hamuli. On gills of marine teleosts.

Key to species of *Gyrodactyloides*

1 Sclerotized components of haptor well developed; hamuli (89–93 long) about 1/3 of total body length; superficial root 56–62 long; marginal hooks 54–63 long; suction disc width 55–62 ... . *G. petruschewskii* Bykhovsky, 1947 (Fig. 35:2, Table 21)
On gills of *Clupea harengus pallasi* (1); *Mallotus villosus* (2)
Records: 1. Arthur and Arai 1980 (Pac); 2. Pálsson and Beverley-Burton 1983 (Atl)

Sclerotized components of haptor less well developed; hamuli (59–64 long) about 1/4 of total body length; superficial root 33–37 long; marginal hooks 40–52 long; suction disc width 32–41 ... . *G. andriaschewi* Bykhovsky and Polyansky, 1953 (Fig. 35:1, Table 21)
On gills of *Mallotus villosus*
Record: Pálsson and Beverley-Burton 1983 (Atl)

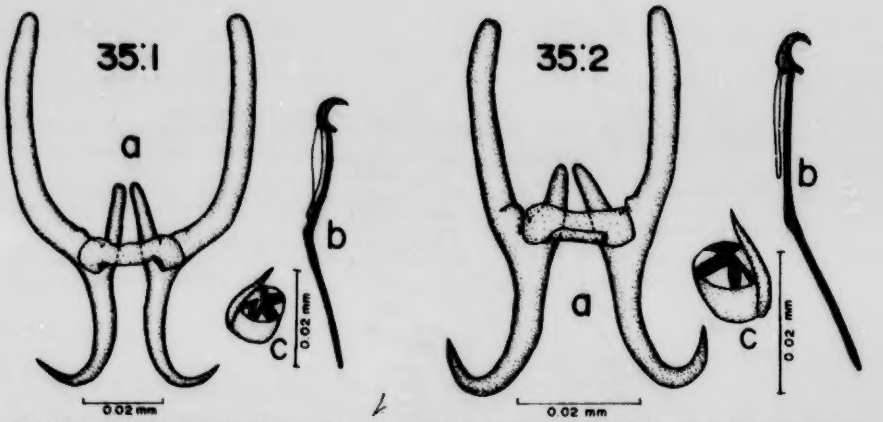

FIG. 35:1–35:2. *Gyrodactyloides* spp. 35:1. *G. andriaschewi* (redrawn from Pálsson and Beverley-Burton 1983): a. hamuli and transverse bar; b. marginal hook; c. penis. 35:2. *G. petruschewskii* (from Pálsson and Beverley-Burton 1983): a. hamuli and transverse bar; b. marginal hook; c. penis.

TABLE 21. Comparative measurements (in μm) of the species of *Gyrodactyloides* Bykhovsky, 1947, and *Laminiscus* Pálsson and Beverley-Burton, 1983, recorded from fishes of Canada.

Species	*G. andriaschewi*	*G. petruschewskii*	*L. gussevi*	*L. strelkowi*
Source of data	Pálsson and Beverley-Burton (1983)	Pálsson and Beverley-Burton (1983)	Pálsson and Beverley-Burton (1983)	Bykhovsky and Polyansky (1953)
Body: length	275 (211–327)	276 (225–325)	381 (329–426)	about 500
width	83 (67–115)	89 (61–114)	107 (75–127)	about 100
Suction disc: width	36 (32–41)	60 (55–62)	—	—
Hamuli: total length	61 (59–64)	90 (86–93)	52 (50–53)	52–59
deep root length	10 (9–12)	16 (14–17)	8 (7–10)	11–13
superficial root length	35 (33–37)	61 (56–62)	25 (23–27)	25–32
shaft length	29 (28–29)	34 (32–37)	39 (38–40)	26–32
point length	10 (9–10)	11 (10–12)	17 (15–18)	14–18
Transverse bar: length	19 (17–22)	25 (24–27)	12 (10–14)	13–14
Marginal hooks (I and VII):				
total length	48 (40–52)	59 (54–63)	34 (32–36)	32–38[a]
sickle length	5.5 (5.2–6.1)	7 (6.2–7.3)	5.5 (5.1–5.8)	—
Penis: diameter	7.6 (7.0–8.0)	8.6 (8.0–9.0)	10.4 (9.0–13.0)	—
spines	1 and 4	1 and 4	1 and 10	—
Site	gills	gills	gills	gills
Host(s)	*Mallotus villosus*	*Clupea harengus pallasi* *Mallotus villosus*	*Mallotus villosus*	*Oncorhynchus gorbuscha* *O. nerka*
Locality(ies)	NW Atlantic	NW Atlantic Pacific	NW Atlantic	Pacific British Columbia (b)

[a] Number of marginal hooks measured not specified.

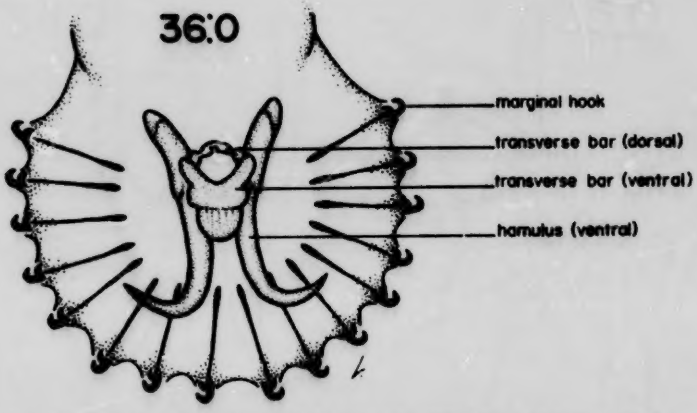

FIG. 36:0. *Gyrodactylus* — haptoral characters (modified from Malmberg 1970).

Gyrodactylus Nordmann, 1832 (Fig. 36:0)

Gyrodactylidae: body elongate with peduncle of normal proportions and lacking an anteriorly directed flange (cf. *Fundulotrema*). Marginal hooks distributed evenly on periphery of haptor. Hamuli with elongate superficial root; ventral and dorsal bars of variable shape. On gills and body surface of freshwater, brackish water, and marine teleosts.

Key to species of *Gyrodactylus*[60,61]

1 Anterolateral processes of ventral bar present (Fig. 36:1a) 2

Anterolateral processes of ventral bar absent (Fig. 36:29a) or, if present, inconspicuous 27

2 Root of hamuli short (Fig. 36:1a). On marine teleosts 3

Root of hamuli elongate (Fig. 36:3a). On freshwater teleosts[62] 6

3 Hamuli 38–43 long .... *G. adspersi* Cone and Wiles, 1983 (Fig. 36:1, Table 27)
On gills, fins, and body surface of *Tautogolabrus adspersus*
Record: Cone and Wiles 1983a (Atl)

Hamuli more than 50 long 4

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[60] Dr David Cone, Department of Biology, St. Mary's University, Halifax, provided expert advice in the design of this key.

[61] Margolis and Arthur (1979) listed *G. medius* Kathariner, 1895 as the species was reported by Cooper (1915) from *Micropterus dolomieui* in Ontario. However, both Price (1937) and Malmberg (1970) considered this to be a misidentification and the record is listed on p. 139 under *Gyrodactylus* spp.

[62] *G. alexanderi*, a parasite of *Gasterosteus aculeatus* with these characteristics, has been found in marine as well as freshwate situations.

4 **Hamuli 63–66 long; membrane broadly ovate ..... *G. groenlandicus* Levinsen, 1881 (Fig. 36:19, Table 27)**
On gills, fins, and body surface of *Myoxocephalus scorpius*
Record: Cone and Wiles 1983a (Atl)

Hamuli 55–59 long; membrane of ventral bar tapered 5

5 Hamuli 56–58 long; marginal hooks 35–36 long .... *G. nainum* Hanek and Threlfall, 1970 (Fig. 36:25, Table 27)
On gills and fins of *Myoxocephalus quadricornis*
Records: Hanek and Threlfall 1970d (Lab-b); Cone and Wiles 1983a (Lab-b)

Hamuli 55–59 long; marginal hooks 27–29 long .... *G. pleuronecti* Cone, 1981 (Fig. 36:28, Table 27)
On gills, fins, and body surface of *Pseudopleuronectes americanus*
Records: Cone 1981 (Nfld-b); Cone and Wiles 1983a (Atl)

6 Membrane of ventral bar relatively large, waisted, with posterior region spatulate (Fig. 36:31a, 36: 33a) 7

Membrane of ventral bar of normal proportions, not waisted, with posterior region not spatulate 8

7 Hamuli 124–130 long; ventral bar 44–46 transverse length, membrane 75–80 long; marginal hooks 51–55 long .... *G. spathulatus* Mueller, 1936 (Fig. 36:31, Table 24)
On gills and fins of *Catostomus catostomus* (3); *C. commersoni* (1,2,4); *Moxostoma anisurum* (2,4)
Records: 1. Dechtiar 1972b (Ont); 2. 1972c (Ont); 3. Threlfall 1974 (Lab); 4. Lubinsky and Loch 1979 (Man)

Hamuli 67–70 long; ventral bar 29–32 transverse length, membrane 36–39 long; marginal hooks 43–48 long .... *G. stunkardi* Kritsky and Mizelle, 1968 (Fig. 36:33, Table 23)
On gills and fins of *Catostomus commersoni* (3); *Etheostoma nigrum* (1); *Rhinichthys atratulus* (1); *R. cataractae* (1,2)
Records: 1. Hanek and Fernando 1971b (Ont); 2. Threlfall 1974 (Lab); 3. Molnar et al. 1974 (Ont)
Remarks: There is no indication which of the listed hosts could be regarded as the primary host genus and which are "accidental" (see remarks on *G. avalonia*, p. 136). It would seem improbable that *G. stunkardi* parasitizes such a broad spectrum of hosts on an equal basis.

8 Anterolateral processes of ventral bar prominent, projecting anteriorly (or anterolaterally) (Fig. 36:12a) 9

Anterolateral processes of ventral bar less prominent, projecting laterally (or anterolaterally) (Fig. 36:27b) 20

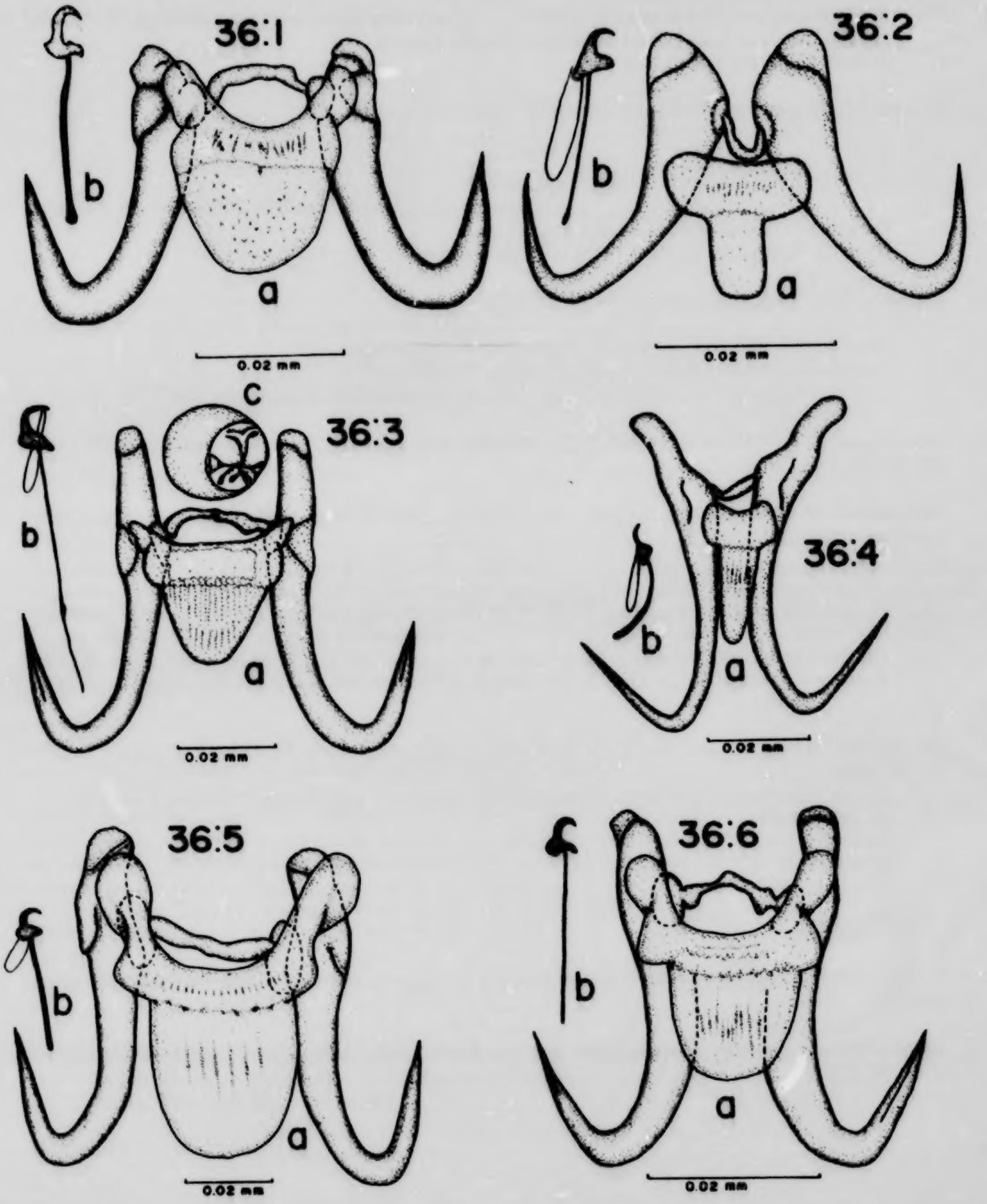


FIG. 36:1–36:6. *Gyrodactylus* spp. 36:1. *G. adspersi* (redrawn from Cone and Wiles 1983a): a. hamuli, dorsal and ventral transverse bars; b. marginal hook. 36:2. *G. aldrichi* (redrawn from Threlfall 1974): a. hamuli, dorsal and ventral transverse bars; b. marginal hook. 36:3. *G. alexanderi* (redrawn from Mizelle and Kritsky 1967a): a. hamuli, dorsal and ventral transverse bars; b. marginal hook; c. penis. 36:4. *G. aquilinus* (redrawn from Threlfall 1974): a. hamuli, dorsal and ventral transverse bars; b. marginal hook. 36:5. *G. atratuli* (redrawn from Threlfall 1974): a. hamuli, dorsal and ventral transverse bars; b. marginal hook. 36:6. *G. avalonia* (redrawn from Hanek and Fernando 1971b): a. hamuli, dorsal and ventral transverse bars; b. marginal hook.

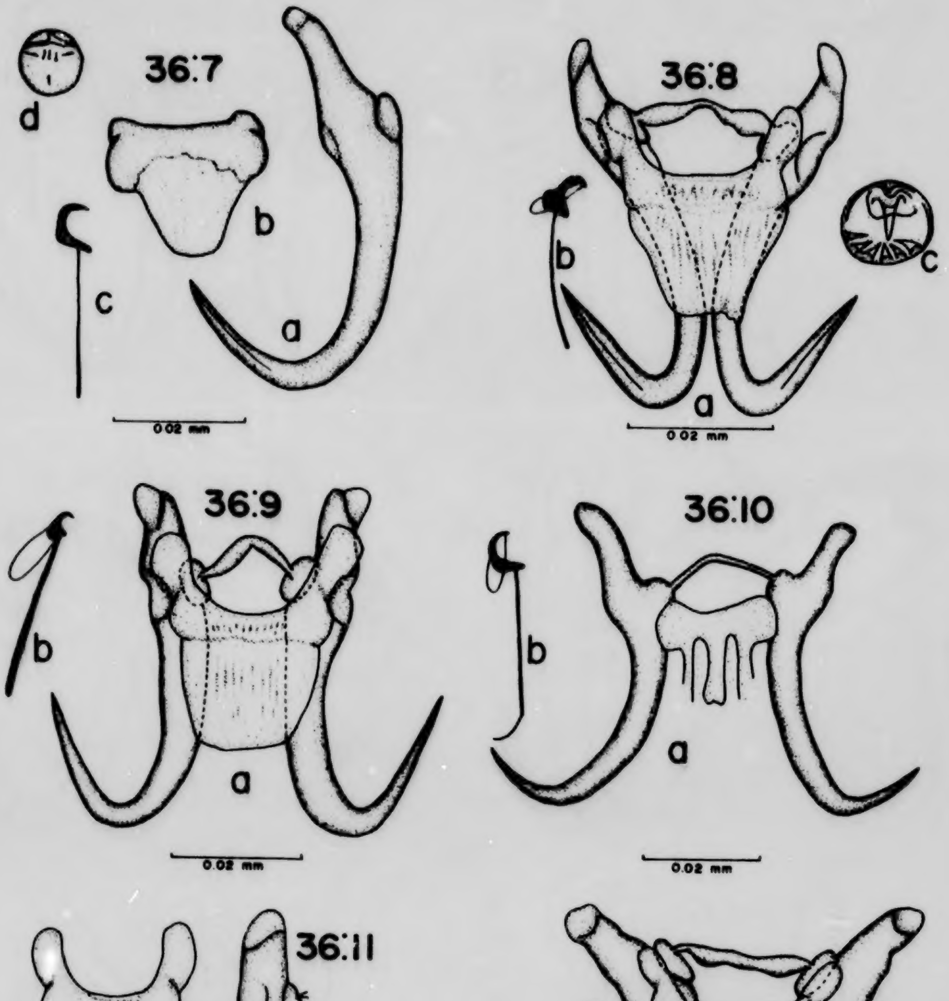

36:7
d
b
c
a
0.02 mm
36:8
b
c
a
0.02 mm
36:9
b
a
0.02 mm
36:10
b
a
0.02 mm
36:11
b
c
a
0.02 mm
36:12
b
a
0.02 mm

FIG. 36:7–36:12. *Gyrodactylus* spp. 36:7. *G. bairdi* (redrawn from Cone and Wiles 1983b): a. hamulus; b. ventral transverse bar; c. marginal hook; d. penis. 36:8. *G. bullatarudis* (redrawn from Turnbull 1956): a. hamuli, dorsal and ventral transverse bars; b. marginal hook; c. penis. 36:9. *G. cameroni* (redrawn from Hanek and Threlfall 1970a): a. hamuli, dorsal and ventral transverse bars; b. marginal hook. 36:10. *G. canadensis* (redrawn from Hanek and Threlfall 1969): a. hamuli, dorsal and ventral transverse bars; b. marginal hook. 36:11. *G. colemanensis* (redrawn from Cone et al. 1983): a. hamulus; b. ventral transverse bar; c. marginal hook. 36:12. *G. commersoni* (redrawn from Threlfall 1974): a. hamuli, dorsal and ventral transverse bars; b. marginal hook.

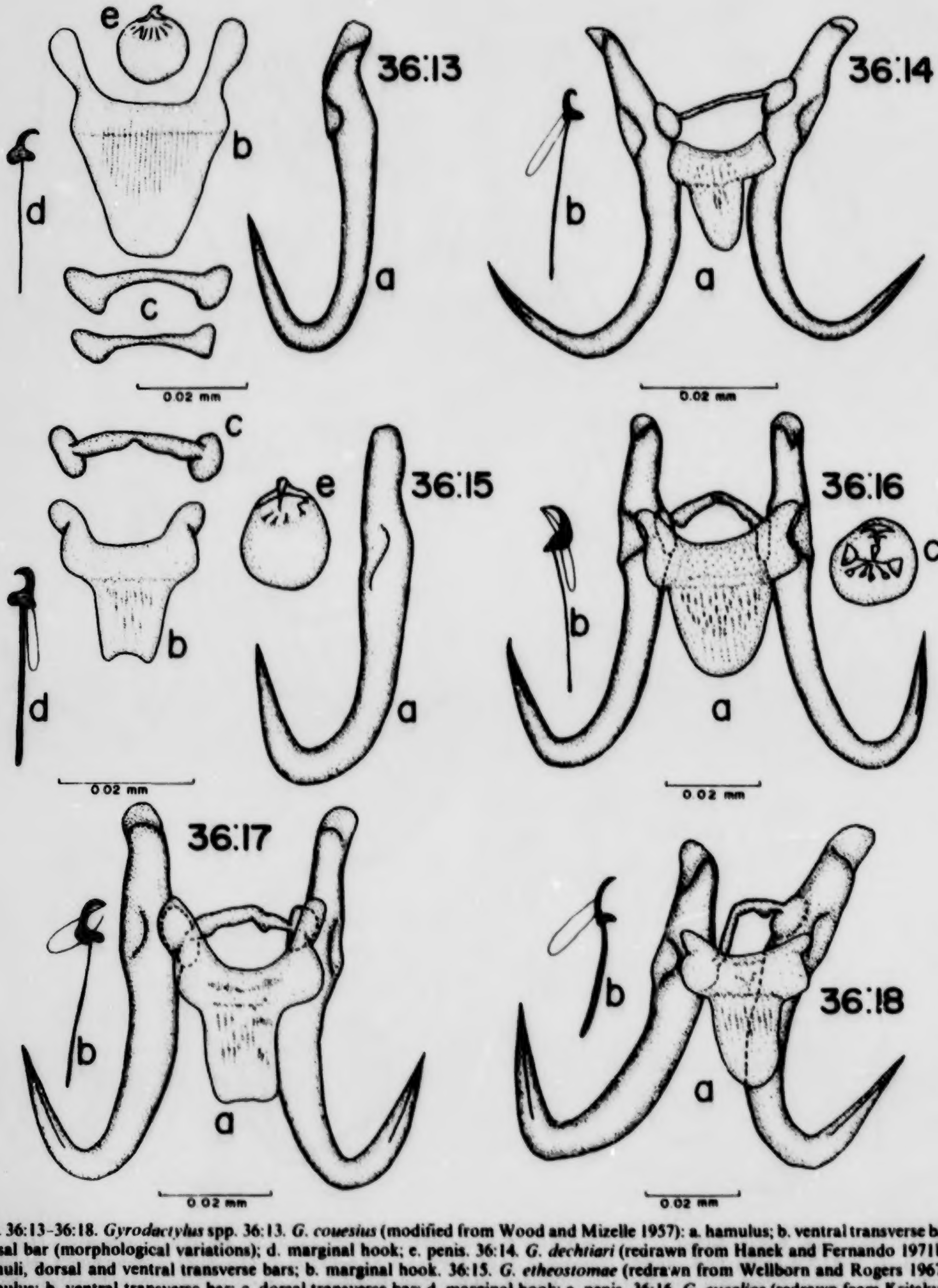
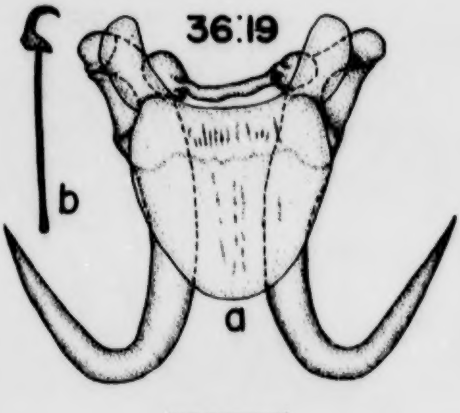
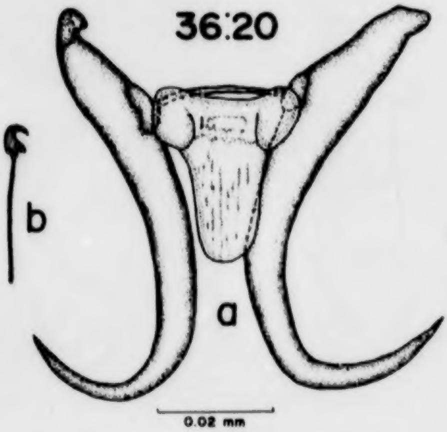
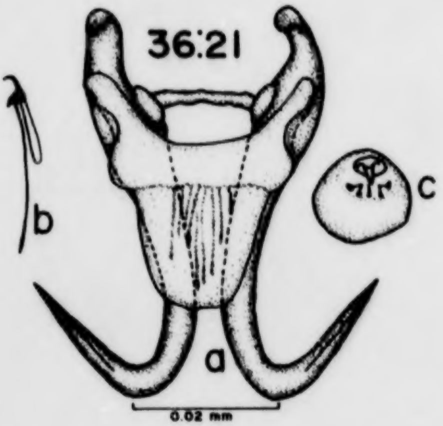
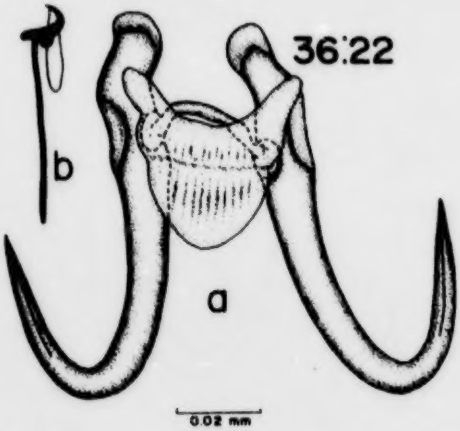

e
36:13
b
d
c
a
0.02 mm
36:14
b
a
0.02 mm
c
e
36:15
b
d
a
0.02 mm
36:16
b
c
a
0.02 mm
36:17
b
a
0.02 mm
b
36:18
a
0.02 mm

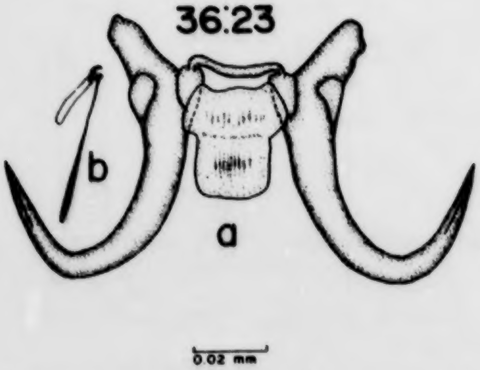
FIG. 36:13–36:18. *Gyrodactylus* spp. 36:13. *G. couesius* (modified from Wood and Mizelle 1957): a. hamulus; b. ventral transverse bar; c. dorsal bar (morphological variations); d. marginal hook; e. penis. 36:14. *G. dechtiari* (redrawn from Hanek and Fernando 1971b): a. hamuli, dorsal and ventral transverse bars; b. marginal hook. 36:15. *G. etheostomae* (redrawn from Wellborn and Rogers 1967): a. hamulus; b. ventral transverse bar; c. dorsal transverse bar; d. marginal hook; e. penis. 36:16. *G. eucaliae* (redrawn from Kritsky and Mizelle 1968): a. hamuli, dorsal and ventral transverse bars; b. marginal hook; c. penis. 36:17. *G. freemani* (redrawn from Hanek and Fernando 1971b): a. hamuli, dorsal and ventral transverse bars; b. marginal hook. 36:18. *G. goerani* (redrawn from Hanek and Fernando 1971b): a. hamuli, dorsal and ventral transverse bars; b. marginal hook.











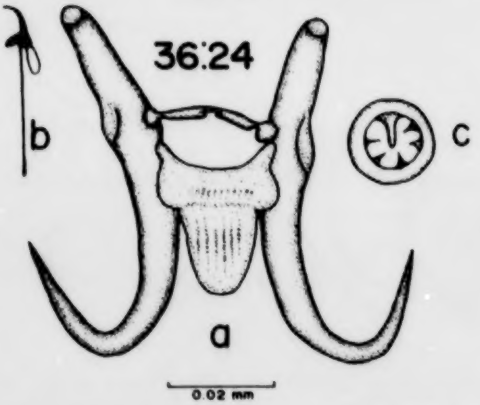
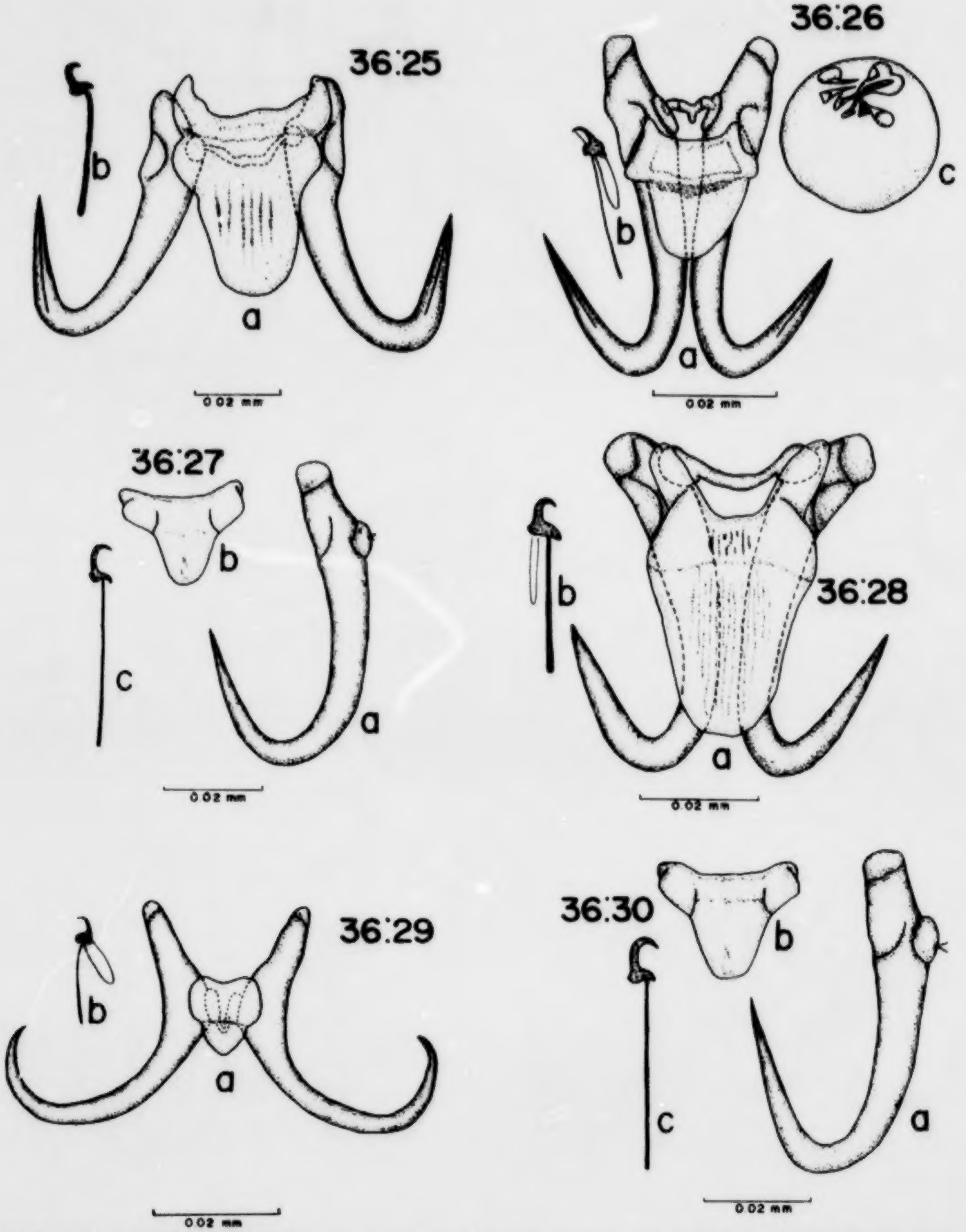


FIG. 36:19–36:24. *Gyrodactylus* spp. 36:19. *G. groenlandicus* (redrawn from Cone and Wiles 1983a): a. hamuli, dorsal and ventral transverse bars; b. marginal hook. 36:20. *G. harengi* (a. redrawn from Zhukov 1960; b. from Malmberg 1970): a. hamuli, dorsal and ventral transverse bars; b. marginal hook. 36:21. *G. hoffmani* (redrawn from Mizelle and Kritsky 1967b): a. hamuli, dorsal and ventral transverse bars; b. marginal hook; c. penis. 36:22. *G. lacusgrandis* (redrawn from Hanek and Threlfall 1970d): a. hamuli, dorsal and ventral transverse bars; b. marginal hook. 36:23. *G. limi* (redrawn from Hanek and Fernando 1971b): a. hamuli, dorsal and ventral transverse bars; b. marginal hook. 36:24. *G. macrochiri* (redrawn from Hoffman and Putz 1964): a. hamuli, dorsal and ventral transverse bars; b. marginal hook; c. penis.


36:25
b
a
0.02 mm
36:26
c
b
a
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36:27
b
c
a
0.02 mm
b
36:28
a
0.02 mm
36:29
b
a
0.02 mm
36:30
b
c
a
0.02 mm

FIG. 36:25–36:30. *Gyrodactylus* spp. 36:25. *G. nainum* (redrawn from Hanek and Threlfall 1970d): a. hamuli, dorsal and ventral transverse bars; b. marginal hook. 36:26. *G. nebulosus* (redrawn from Kritsky and Mizelle 1968): a. hamuli, dorsal and ventral transverse bars; b. marginal hook; c. penis. 36:27. *G. nerkae* (redrawn from Cone et al. 1983): a. hamulus; b. ventral transverse bar; c. marginal hook. 36:28. *G. pleuronecti* (redrawn from Cone 1981): a. hamuli, dorsal and ventral transverse bars; b. marginal hook. 36:29. *G. plumbeae* (redrawn from Threlfall 1974): a. hamuli, dorsal and ventral transverse bars; b. marginal hook. 36:30. *G. salmonis* (redrawn from Cone et al. 1983): a. hamulus; b. ventral transverse bar; c. marginal hook.

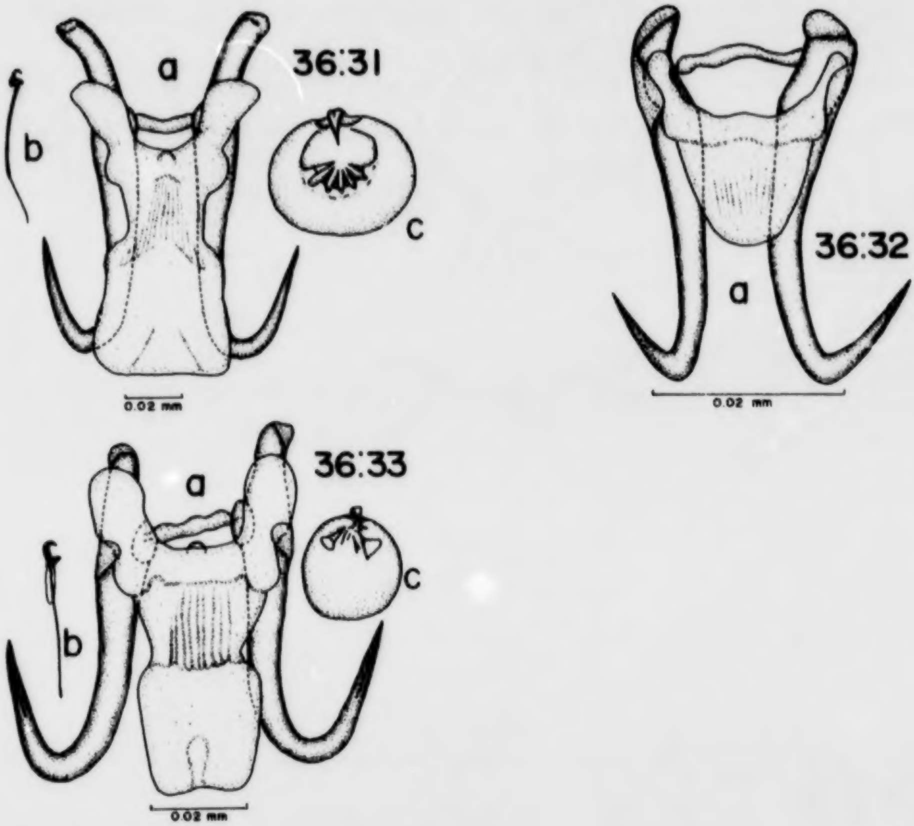

FIG. 36:31–36:33. *Gyrodactylus* spp. 36:31. *G. spathulatus* (redrawn from Mueller 1936a): a. hamuli, dorsal and ventral transverse bars; b. marginal hook; c. penis. 36:32. *G. stephanus* (redrawn from Hargis 1955): a. hamuli, dorsal and ventral transverse bars. 36:33 *G. stunkardi* (redrawn from Kritsky and Mizelle 1968): a. hamuli, dorsal and ventral transverse bars; b. marginal hook; c. penis.

9 Hamuli slender, points not sharply reflected ....
.. *G. commersoni* Threlfall, 1974 (Fig. 36:12, Table 24)
On gills of *Catostomus commersoni*
Record: Threlfall 1974 (Lab)

Hamuli robust, points sharply reflected (Fig. 36:22a) 10

10 Hamuli 79–81 long; marginal hooks 44–46 long ....
.... *G. lacusgrandis* Hanek and Threlfall, 1970 (Fig. 36:22, Table 25)
On fins of *Cottus bairdi*
Record: Hanek and Threlfall 1970d (Lab)

Hamuli not more than 74 long; marginal hooks not more than 36 long 11

TABLE 22. Comparative measurements (in μm) of the species of *Gyrodactylus* Nordmann, 1832, recorded from Salmoniformes (Salmonidae[a] and Umbridae) of Canada.

Species	*G. colemanensis*	*G. nerkae*	*G. salmonis*	*G. limi*
Source of data	Cone et al. (1983)[b]	Cone et al. (1983)	Cone et al. (1983)	Hanek and Fernando (1971b)
Body: length	—	300 (250–390)[c]	420–540[d]	1080
width	—	70 (56–120)	112–180	192
Hamuli: total length	43–48	61 (57–67)	58–62	73
root length	9–12	20 (18–23)	17–21	19
shaft length	32–35	47 (44–49)	44–53	63
point length	19–21	32 (31–34)	33–35	34
Dorsal bar: transverse length	15–20	20 (20–28)	up to 28	28
Ventral bar: transverse length	22–26	24 (19–26)	22–28	29
anterolateral proc.	8–9	2 (2–3)	2–3	lacking
membrane length	10–12	13 (10–13)	8–14	14
Marginal hooks: total length	26–29	41 (40–45)	41–45	45
sickle length	5–6	9 (8–9)	8–9	4
Penis: diameter	—	16 (11–16)	11–16	18
Site	body surface	body surface	body surface	fins
Host(s)	*Salmo gairdneri*[e] *Salvelinus fontinalis*	*Oncorhynchus nerka*	*Oncorhynchus kisutch* *Salmo clarki*[e] *S. gairdneri* *S. salar* *Salvelinus fontinalis*	*Umbra limi*
Locality(ies)	Newfoundland Nova Scotia	British Columbia	British Columbia Nova Scotia	Ontario

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[a] Threlfall and Hanek (1970b) recorded *G. avalonia* Hanek and Threlfall, 1969 from *Salvelinus fontinalis*. Cone et al. (1983) regarded *G. avalonia* as a parasite of sticklebacks, and of accidental occurrence on *S. fontinalis* (see Table 26).

[b] Measurement of worms from type host in Newfoundland.

[c] Holotype and, in parentheses, range.

[d] Measurements of worms from *S. clarki*.

[e] Type host.

TABLE 23. Comparative measurements (in μm) of the species of *Gyrodactylus* Nordmann, 1832, recorded from cyprinid fishes of Canada.

Species	*G. aldrichi*	*G. atratuli*	*G. couesius*	*G. dechtiari*	*G. hoffmani*	*G. plumbeae*	*G. stunkardi*
Source of data	Threlfall (1974)	Hanek and Fernando (1971b)	Wood and Mizelle (1957)	Hanek and Fernando (1971b)	Wellborn and Rogers (1967)	Threlfall (1974)	Hanek and Fernando (1971b)
Body: length	840 (620–840)[a]	465–768[b]	314 (242–386)	480 (408–516)[d]	374 (350–500)	444 (348–560)[a]	544–810[b]
width	72 (60–91)	70–96	90 (72–106)	96 (80–110)	82 (60–100)	120 (94–135)	87–144
Hamuli: length	33 (33–35)	58–68	61 (58–65)	45 (43–49)	48 (43–54)	39 (37–39)	67–70
root length	10 (9–10)	16–22	—	17 (15–19)	—	16 (14–16)	20–23
shaft length	27 (26–27)	41–46	—	34 (33–36)	—	31 (30–32)	48–52
point length	15 (13–15)	26–31	—	20 (18–22)	23 (20–25)	13 (12–13)	29–32
Dorsal bar: transverse length	10 (8–10)	19–22	26 (24–33)	13 (12–14)	20 (18–24)	11 (10–12)	23–26
Ventral bar: transverse length	14 (12–14)	26–30	35 (31–47)	14 (14–15)	21 (18–25)	12 (11–13)	29–32
anterolateral proc.	lacking	11–14	—	lacking	9 (6–11)	5 (5–6)	14–16
membrane (length)	6 (6–9)	14–24	—	14 (13–16)	16 (14–17)	lacking	36–39
Marginal hooks: total length	22 (22)	29–36	31 (29–33)	28 (28–29)	24–28	17 (16–17)	43–48
sickle length	5 (5)	4–6	—	4 (4–5)	5–6	4 (4)	6
Penis: diameter	19 (15–19)	15–16	—	10 (10–11)	13	13 (14–16)	17–18
Site(s)	gills	fins	gills	gills	fins	gills	fins, gills
Host(s)	*Couesius plumbeus*	*Catostomus catostomus*[c] *Rhinichthys atratulus* *R. cataractae*	*Couesius plumbeus*	*Rhinichthys atratulus*[e] *R. cataractae*	*Pimephales promelas*	*Couesius plumbeus*	*Catostomus commersoni*[f] *Etheostoma nigrum* *Rhinichthys atratulus* *R. cataractae*
Locality(ies)	Labrador	Labrador Ontario	British Columbia	Ontario	Ontario	Labrador	Ontario Labrador

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[a] Holotype and, in parentheses, paratypes.

[b] Measurements of worms from both *Rhinichthys* spp. combined.

[c] "Accidental" infection? See remarks on *G. atratuli* on p. 136.

[d] Holotype (from *R. atratulus*) followed in parentheses by measurements from both host species combined.

[e] Type host.

[f] See remarks on *G. stunkardi* on p. 123.

TABLE 24. Comparative measurements (in μm) of the species of *Gyrodactylus* Nordmann, 1832, recorded from catostomids, ictalurids and poeciliids of Canada.

Species	*G. aquilinus*	*G. spathulatus*	*G. commersoni*	*G. nebulosus*	*G. bullatarudis*
Source of data	Threlfall (1974)	Threlfall (1974)	Threlfall (1974)	Hanek and Fernando (1971b)	Turnbull (1956)
Body: length	672 (530–672)[a]	500–710	672 (481–720)[a]	557–720	405 (301–443)[a]
width	96 (60–96)	90–111	120 (78–120)	45–72	68 (53–97)
Hamuli: total length	62 (61–62)	124–130	56 (56–58)	50–52	51 (48–54)
root length	21 (20–21)	43–46	17 (15–17)	14–15	—
shaft length	47 (45–47)	85–91	48 (47–48)	37–39	—
point length	26 (25–27)	40–43	21 (20–22)	26–29	23–25
Dorsal bar: transverse length	10 (9–12)	28–30	23 (21–23)	13	22 (20–25)
Ventral bar: transverse length	16 (15–17)	44–46	25 (24–26)	17	23 (22–25)
anterolateral proc.	lacking	28–30	6 (6–7)	lacking	9 (14–17)
membrane length	19 (16–19)	75–80	19 (19–21)	14–15	14
Marginal hooks: total length	22 (22)	51–55	26 (26)	26–27	26 (24–27)
sickle length	6 (6)	6–7	5 (5)	5–6	6 (5–6)
Penis: diameter	12 (12–13)	15–27	16 (13–16)	9	12 (11–16)
Site(s)	fins	gills, fins	gills	fins	fins, skin
Host(s)	*Catostomus catostomus*	*Catostomus commersoni* *C. catostomus* *Moxostoma anisurum*	*Catostomus commersoni*	*Ictalurus nebulosus*	*Poecilia reticulata*[b]
Locality(ies)	Labrador	Labrador Manitoba Ontario	Labrador	Ontario	Ontario

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[a] Holotype and, in parentheses, range. For Turnbull's (1956) *G. bullatarudis*, the range is for paratypes only and does not include measurements of the holotype.

[b] Aquarium host.

TABLE 25. Comparative measurements (in μm) of the species of *Gyrodactylus* Nordmann, 1832, recorded from Perciformes (Centrarchidae, Percidae, and Cottidae) of Canada.

Species	*G. goerani*	*G. macrochiri*	*G. etheostomae*	*G. freemani*	*G. bairdi*	*G. lacusgrandis*
Source of data	Hanek and Fernando (1971b)	Hanek and Fernando (1971b)	Hanek and Fernando (1971b)	Hanek and Fernando (1971b)	Wood and Mizelle (1957)	Hanek and Threlfall (1970d)
Body: length	510 (480–586)[a]	515–810[b]	470–712[c]	840 (644–864)[a]	368 (296–404)	—
width	92 (80–106)	89–142	61–100	120 (84–125)	72 (36–108)	—
Hamuli: total length	78 (75–78)	63–69	57–74	67 (67–71)	68 (65–70)[d]	79 (79–81)[a]
root length	23 (23–25)	19–22	18–27	25 (23–25)	—	25 (24–25)
shaft length	55 (52–55)	45–51	41–53	51 (51–52)	—	55 (55–56)
point length	32 (30–32)	27–30	25–29	30 (27–30)	—	35 (34–36)
Dorsal bar: transverse length	25 (23–26)	23–26	18–27	19 (19–22)	16 (14–18)	24 (24–26)
Ventral bar: transverse length	27 (27–28)	26–29	22–29	28 (25–28)	24 (20–26)	27 (26–27)
anterolateral proc.	4 (3–4)	4	3–8	10 (9–10)	—	9 (8–9)
membrane length	22 (22–23)	14–18	11–28	19 (17–19)	—	20 (19–21)
Marginal hooks: total length	39 (39–40)	35–37	28–33	35 (34–35)	—	45 (44–46)
sickle length	10	8	6–8	8	8	8
Penis: diameter	16	17–19	15	26	9 (8–11)	—
Site(s)	fins	gills, fins	fins	fins	gills	fins
Host(s)	*Ambloplites rupestris*	*Lepomis gibbosus* *Micropterus dolomieui* *M. salmoides*	*Etheostoma exile* *E. nigrum*	*Perca flavescens*	*Cottus bairdi* *C. cognatus*	*Cottus bairdi*
Locality(ies)	Ontario	Manitoba Ontario	Ontario	Ontario	Labrador Manitoba Ontario Yukon Territory	Labrador

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[a] Holotype and, in parentheses, paratypes.

[b] Measurements of worms from *M. dolomieui* and *M. salmoides* combined.

[c] Hanek and Fernando (1971b) provide two sets of measurements for material from smaller (less than 3 mm) and larger (greater than 3 mm) *E. nigrum* which are herein combined.

[d] See also Cone and Wiles (1983b).

TABLE 26. Comparative measurements (in μm) of the species of *Gyrodactylus* Nordmann, 1832, recorded from Gasterosteiformes of Canada.[a]

Species	*G. alexanderi*	*G. avalonia*[a]	*G. cameroni*	*G. canadensis*	*G. eucaliae*	*G. stephanus*[d]
Source of data	Mizelle and Kritsky (1967a)	Hanek and Fernando (1971b)	Hanek and Threlfall (1970a)	Hanek and Threlfall (1969)	Hanek and Fernando (1971b)	Hargis (1955)
Body: length	698 (598–841)	615–710[b]	—	—	520–782	328 (299–357)
width	128 (97–204)	94–127	—	—	94–120	44 (38–51)
Hamuli: total length	79 (72–82)	37–43	50–53	55–56	69–73	42 (39–44)
root length	—	10–13	12–13	18–19	21–25	—
shaft length	—	30–32	40–41	43–45	52–53	—
point length	—	17–18	23–24	13–14	26–28	—
Dorsal bar: transverse length	18 (14–27)	17–18	21–22	21–22	21–25	16
Ventral bar: transverse length	40 (37–44)	19–20	25–26	24–25	28–30	20 (19–20)
anterolateral proc.	—	8–9	—	lacking	4–6	—
membrane length	—	12-13	16–17	—	18–21	"delicate"
Marginal hooks: total length	43 (42–44)	21–23	29	40–41	36	23[e]
sickle length	11 (10–12)	4	5	7–8	8	—
Penis: diameter	20	17	—	—	15	8
Site(s)	skin	gills, fins	fins	gills	gills, fins	gills
Host(s)	*Gasterosteus aculeatus*	*Apeltes quadracus* *Fundulus diaphanus* *Gasterosteus aculeatus*[c] *G. wheatlandi* *Lepomis gibbosus* *Pungitius pungitius* *Rhinichthys atratulus* *Salmo gairdneri* *Salvelinus fontinalis*	*Apeltes quadracus*	*Apeltes quadracus* *Gasterosteus aculeatus* *Pungitius pungitius*	*Culaea inconstans*	*Fundulus heteroclitus*[c] *Pungitius pungitius*
Locality(ies)	Pacific British Columbia	Atlantic Labrador Newfoundland Nova Scotia Ontario Quebec	Newfoundland	Atlantic Labrador Newfoundland Quebec	Manitoba Ontario	Newfoundland

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[a] *G. avalonia* is regarded as a parasite of gasterosteids which may occur on other hosts.

[b] Material from *G. aculeatus* (type host) taken in Ontario.

[c] Type host.

[d] The type host of *G. stephanus* was listed as *Fundulus heteroclitus* by Mueller (1937). However, it is included in this table as it was recorded from a stickleback by Dickinson and Threlfall (1976).

[e] From Mueller (1937).

TABLE 27. Comparative measurements (in μm) of the species of *Gyrodactylus* Nordmann, 1832, reported from marine fishes of Canada.

Species	*G. adspersi*	*G. groenlandicus*	*G. harengi*	*G. nainum*	*G. pleuronecti*
Source of data	Cone and Wiles (1983a)	Cone and Wiles (1983a)	Zhukov (1960)	Cone and Wiles (1983a)	Cone (1981)
Body: length	460 (379–592)[a]	468–546	310–410	910[b]	450 (400–510)[a]
width	132 (110–190)	120–156	75–83	162	95 (80–110)
Hamuli: total length	39 (38–43)	63–66	40–47	59 (56–58)	58 (55–59)
root length	(9–12)	13–16	12–18	15 (12–14)	10 (10–13)
shaft length	35 (33–36)	56–59	29–36	50	51 (47–53)
point length	21 (21–24)	35–36	14–16	29 (27–29)	31 (29–32)
Dorsal bar: transverse length	21 (19–21)	31–35	12–14	—	24 (24–31)
Ventral bar: transverse length	21 (18–24)	32–34	18	—	27 (25–28)
anterolateral proc.	6 (6–9)	10–12	lacking	—	—
membrane length	17 (13–17)	28–32	—	—	29 (26–30)
Marginal hooks: total length	25–26 (24–27)	35–36	27–29	35–36 (35–36)	28 (27–29)
sickle length	5 (5–6)	7–8	—	7–8 (7–8)	7 (7)
Penis: diameter	14 (14–17)	13–15	—	—	19 (19–21)
Site(s)	gills, fins body surface	gills, fins body surface	gills	gills, fins	gills, fins body surface
Host	*Tautogolabrus adspersus*	*Myoxocephalus scorpius*	*Clupea harengus pallasi*	*Myoxocephalus quadricornis*	*Pseudopleuronectes americanus*
Locality(ies)	Atlantic	Atlantic	British Columbia Pacific	Labrador	Newfoundland

[a] Holotype and, in parentheses, range.
[b] Measurements of holotype from Cone and Wiles (1983a) and paratypes from Hanek and Thelfall (1970d) in parentheses.

11 **On exotic aquarium guppies (*Poecilia reticulata*) .... *G. bullatarudis* Turnbull, 1956 (Fig. 36:8, Table 24)**

On fins and body surface of exotic aquarium guppies (*Poecilia reticulata*)
Record: Turnbull 1956
Remarks: *G. bullatarudis* was described by Turnbull (1956) from material found on a tropical guppy, *Poecilia reticulata*, held in an aquarium in Ontario. *G. bullatarudis* has since been used experimentally in aquarium situations and has been recorded from wild populations of guppies in Central America.

On wild freshwater and brackish water fishes 12

12 **Hamuli not less than 57 long 13**

Hamuli not more than 54 long 16

13 **On percids 14**

On cyprinids 15

14 Hamuli 57–74 long; ventral bar 22–29 transverse length, anterolateral processes 3–8 long; marginal hooks 28–33 long .... *G. etheostomae* Wellborn and Rogers, 1967 (Fig. 36:15, Table 25)

On fins of *Etheostoma exile* (2); *E. nigrum* (1)
Records: 1. Hanek and Fernando 1971b (Ont); 2. Molnar et al. 1974 (Ont)

Hamuli 67–71 long; ventral bar 25–28 transverse length, anterolateral processes 9–10 long; marginal hooks 34–35 long .... *G. freemani* Hanek and Fernando, 1971 (Fig. 36:17, Table 25)

On fins of *Perca flavescens*
Record: Hanek and Fernando 1971b (Ont)

15 Ventral bar 26–30 transverse length, membrane ovate posteriorly .... *G. atratuli* Putz and Hoffman, 1963 (Fig. 36:5, Table 23)

On fins of *Catostomus catostomus* (2); *Rhinichthys atratulus* (1); *R. cataractae* (1)
Records: 1. Hanek and Fernando 1971b (Ont); 2. Threlfall 1974 (Lab)
Remarks: *Rhinichthys* spp. are probably the primary hosts for *G. atratuli* while *Catostomus commersoni* may be an "accidental" host. Threlfall (1974) found a low prevalence (5%) and intensity (1-6) on *C. commersoni* taken from the same location as *R. cataractae*, which may have been infected with *G. atratuli*.

Ventral bar 31–47 transverse length, membrane tapered posteriorly .... *G. couesius* Wood and Mizelle, 1957[63] (Fig. 36:13, Table 23)

On gills of *Couesius plumbeus*
Record: Wood and Mizelle 1957 (BC)

16 Pimarily on gasterosteids. Root of hamulus in line with shaft, not reflected medianly (Fig. 36:9a) 17

Primarily on fishes other than gasterosteids (salmonids, a cyprinid, and *Fundulus* spp.). Root of hamulus reflected medianly (Fig. 36:32a) or not 18

17 Hamuli 37–43 long; ventral bar 19–20 transverse length; marginal hooks 21–23 long .... *G. avalonia* Hanek and Threlfall, 1969 (Fig. 36:6, Table 26)

Syn: *G. lairdi* Hanek and Threlfall, 1969 (new syn.)
G. memorialis Hanek and Threlfall, 1969 (new syn.)
G. terranovae Hanek and Threlfall, 1969 (new syn.)
On gills and fins of *Apeltes quadracus* (2); *Fundulus diaphanus* (7); *Gasterosteus aculeatus* (1,4,7,8); *G. wheatlandi* (1,5); *Lepomis gibbosus* (7); *Pungitius pungitius* (3,8); *Rhinichthys atratulus* (7); *Salmo gairdneri* (9); *Salvelinus fontinalis* (6)
Records: 1. Hanek and Threlfall 1969 (Nfld-b); 2. 1970a (Nfld-b); 3. 1970b (Lab-b, Nfld); 4. 1970c (Atl, Lab-b, Lab, Nfld-b, Nfld); 5. 1971 (Nfld-b); 6. Threlfall and Hanek 1970b (Nfld-b); 7. Hanek and Fernando 1971b (Ont); 8. Hanek and Molnar 1974 (Que-b, Que); 9. Cone et al. 1983 (NS)
Remarks: Synonymy proposed by Cone (pers. comm.). Malmberg (1970) noted the high degree of host specificity seen in *Gyrodactylus* spp. and that few species occur on two or more host species. Where this has been reported, Malmberg (1970) considered that "wrong" hosts are involved and that they are only infected during particular periods of the year or under "special circumstances". Cone et al. (1983) believed sticklebacks (Gasterosteidae) are the primary hosts for *G. avalonia* and the other listed hosts (which represent four families of fishes) are accidental.

Hamuli 50–53 long; ventral bar 25–26 transverse length, marginal hooks 29 long .... *G. cameroni* Hanek and Threlfall, 1970 (Fig. 36:9, Table 26)

On fins of *Apeltes quadracus*
Record: Hanek and Threlfall 1970a (Nfld-b)

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[63] Based on material from the collection of Bangham and Adams (1954) (Adams 1984, pers. comm.).

18 **On salmonids. Root of hamulus not reflected medianly** .... *G. colemanensis* **Mizelle and Kritsky, 1967 (Fig. 36:11, Table 22)**
On skin of *Salmo gairdneri* and *Salvelinus fontinalis*
Record: Cone et al. 1983 (Nfld, NS)

On fishes other than salmonids. Root of hamulus reflected medianly **19**

19 **Primarily on gills of *Fundulus* spp. Hamuli 39–44 long; ventral bar 19–20 transverse length; marginal hooks 23 long** .... *G. stephanus* **Mueller, 1937 (Fig. 36:32, Table 26)**
On gills of *Fundulus heteroclitus* (1); *Pungitius pungitius* (2)
Records: 1. Dickinson and Threlfall 1975 (Nfld); 2. 1976 (Nfld)
Remarks: *G. stephanus* was reported from *F. heteroclitus* taken in Maryland, U.S.A. and *F. grandis* taken in Florida, U.S.A. by Mueller (1937) and Hargis (1955), respectively, as well as in Newfoundland. Thus, *G. stephanus* is regarded as being an "accidental" parasite of *P. pungitius* (see remarks on *G. avalonia*, p. 136).

On fins of *Pimephales promelas*. Hamuli 43–54 long; ventral bar 18–25 transverse length; marginal hooks 24–28 long .... *G. hoffmani* **Wellborn and Rogers, 1967 (Fig. 36:21, Table 23)**
On fins of *Pimephales promelas*
Record: Molnar et al. 1974 (Ont)

20 **On salmonids** **21**

On fishes other than salmonids (Perciformes, centrarchids, cottids, ictalurids or gasterosteids) ... **22**

21 **Marginal hooks 40–45 long, sickle 8–9 long with relatively slender blade, filament loop 12–14 long** .... *G. nerkae* **Cone, Beverley-Burton, Wiles and McDonald, 1983 (Fig. 36:27, Table 22)**
On body surface of *Oncorhynchus nerka*
Record: Cone et al. 1983 (BC)

Marginal hooks 41–45 long, sickle 8–9 long with relatively broad blade, filament loop 14–16 long ... . *G. salmonis* **Yin and Sproston, 1948 (Fig. 36:30, Table 22)**
On body surface of *Oncorhynchus kisutch, Salmo clarki, S. gairdneri, S. salar, Salvelinus fontinalis*
Record: Cone et al. 1983 (BC, NS)

22 **Hamuli 50–52 long; marginal hooks 26–27 long, sickle 5–6 long** .... *G. nebulosus* **Kritsky and Mizelle, 1968 (Fig. 36:26, Table 24)**
On fins of *Ictalurus nebulosus*
Records: Hanek and Fernando 1971b (Ont); Molnar et al. 1974 (Ont)

Hamuli 63 or more long; marginal hooks 35 or more long, sickle 8 or more long **23**

23 **Sickle of marginal hooks crescent-shaped, lacking a basal "heel". On gills of *Cottus* spp.** ... . *G. bairdi* **Wood and Mizelle, 1957 (Fig. 36:7, Table 25)**
Syn: *G. labradorius* Hanek and Threlfall, 1970
On gills of *Cottus bairdi* (1,2,3,5); *C. cognatus* (4)
Records: 1. Hanek and Threlfall 1970d (Lab); 2. Dechtiar 1972b (Ont); 3. 1972c (Ont); 4. Arthur et al. 1976 (YT); 5. Lubinsky and Loch 1979 (Man)
Remarks: Synonymy proposed by Cone and Wiles (1983b).

Sickle of marginal hooks not crescent-shaped, with distinct basal heel. Not on gills of *Cottus* spp. **24**

24 On centrarchids 25

On gasterosteids 26

25 Hamuli 75–78 long; marginal hooks 39–40 long, sickle 10 long ....
.... *G. goerani* Hanek and Fernando, 1971 (Fig. 36:18, Table 25)
On fins of *Ambloplites rupestris*
Record: Hanek and Fernando 1971b (Ont)

Hamuli 63–69 long; marginal hooks 35–37 long, sickle 8 long ....
.... *G. macrochiri* Hoffman and Putz, 1964 (Fig. 36:24, Table 25)
On gills and fins of *Lepomis gibbosus* (2,4); *Micropterus dolomieui* (1); *M. salmoides* (1,3)
Records: 1. Hanek and Fernando 1971b (Ont); 2. Dechtiar 1972c (Ont); 3. Molnar et al. 1974 (Ont); 4. Lubinsky and Loch 1979 (Man)
Remarks: *G. macrochiri* was proposed for worms found on *Lepomis macrochirus* and *L. cyanellus* in West Virginia and Pennsylvania, U.S.A. Hoffman and Putz (1964) experimentally infected *Micropterus salmoides, Salmo gairdneri, Salvelinus fontinalis,* and *Cottus bairdi*, with *G. macrochiri* but all infections were light on these "abnormal" hosts. Cone et al. (1983) commented that *G. macrochiri* has never been reported from either wild or cultured salmonids and is naturally specific to centrarchids.

26 Hamuli 72–82 long; marginal hooks 42–44 long, sickle 10–12 long ....
.... *G. alexanderi* Mizelle and Kritsky 1967 (Fig. 36:3, Table 26)
On body surface of *Gasterosteus aculeatus*
Records: Lester 1972 (BC); 1974 (Pac, BC); Lester and Adams 1974 (Pac, BC)

Hamuli 69–73 long; marginal hooks 36 long, sickle 8 long ....
.... *G. eucaliae* Ikezaki and Hoffman, 1957 (Fig. 36:16, Table 26)
On gills and fins of *Culaea inconstans*
Records: Hanek and Fernando 1971b (Ont); Dechtiar 1972c (Ont); Lubinsky and Loch 1979 (Man)

27 Root and shaft of hamuli strongly curved; marginal hooks with small sickle 28

Root not strongly curved although shaft may be; marginal hooks with relatively large sickle 29

28 Hamuli 37–39 long; marginal hooks 16–17 long ....
.... *G. plumbeae* Threlfall, 1974 (Fig. 36:29, Table 23)
On gills of *Couesius plumbeus*
Record: Threlfall 1974 (Lab)

Hamuli 40–47 long; marginal hooks 27–29 long ....
.... *G. harengi* Malmberg, 1957 (Fig. 36:20, Table 27)
On gills of *Clupea harengus pallasi*
Record: Arthur and Arai 1980 (Pac)
Remarks: Malmberg (1957) proposed *G. harengi* for worms from *Clupea harengus membras* taken in the Baltic. Zhukov (1960) provided morphometric data for *G. harengi* from *C. harengus pallasi* and *Ammodytes hexapterus hexapterus* taken in the Bering Sea. However, Malmberg (1970), having examined specimens from the two last named hosts, stated the worms from *C. harengus pallasi* probably belonged to a different subspecies from those described from *C. harengus membras* and the worms from *A. hexapterus* were not *G. harengi*. Arthur and Arai (1980) found *G. harengi* on *C. harengus pallasi* taken along the B.C. coast and the morphometric data given in Table 27 are from Zhukov (1960).

29 Sickle of marginal hooks with enlarged base and narrow blade; ratio of length:width of ventral bar membrane more than 2:1 .... *G. aquilinus* Threlfall, 1974 (Fig. 36:4, Table 24)

On fins of *Catostomus catostomus*
Record: Threlfall 1974 (Lab)

Sickle of marginal hooks may have enlarged base but blade robust, never narrow; ratio of length: width of ventral bar membrane less than 2:1 30

30 Sickle of marginal hooks crescent-shaped, lacking a basal "heel" 31

Sickle of marginal hooks not crescent-shaped, with distinct basal "heel" 32

31 Hamuli 43–49 long; total length of marginal hooks 28–29, sickle 4–5 .... *G. dechtiari* Hanek and Fernando, 1971 (Fig. 36:14, Table 23)

On gills of *Rhinichthys atratulus, R. cataractae*
Record: Hanek and Fernando 1971b (Ont)

Hamuli 55–56 long; total length of marginal hooks 40–41, sickle 7–8 .... *G. canadensis* Hanek and Threlfall, 1969 (Fig. 36:10, Table 26)

On gills of *Apeltes quadracus* (2); *Gasterosteus aculeatus* (1,4,5); *Pungitius pungitius* (3,5)
Records: 1. Hanek and Threlfall 1969 (Nfld-b); 2. 1970a (Nfld-b); 3. 1970b (Lab-b, Nfld); 4. 1970c (Atl, Nfld-b, Nfld); 5. Hanek and Molnar 1974 (Que-b, Que)
Remarks: Malmberg (1970) considered *G. canadensis* was "a possible synonym" of *G. branchicus* Malmberg, 1964, which was described from worms parasitizing *Gasterosteus aculeatus* taken in brackish and marine waters in Sweden. Studies in progress by Cone (pers. comm.) on the *Gyrodactylus* spp. of sticklebacks will resolve this problem.

32 Hamuli 33–35 long; total length of marginal hooks 22, sickle 5 .... *G. aldrichi* Threlfall, 1974 (Fig. 36:2, Table 23)

On gills of *Couesius plumbeus*
Record: Threlfall 1974 (Lab)

Hamuli 73 long; total length of marginal hooks 45, sickle 4 .... *G. limi* Wood and Mizelle, 1957 (Fig. 36:23, Table 22)

On fins of *Umbra limi*
Record: Hanek and Fernando 1971b (Ont)

Records of unidentified *Gyrodactylus* spp. are listed from:

Ambloplites rupestris — Dechtiar 1972b, 1972c, Ontario, Lubinsky and Loch 1979, Manitoba; *Chrosomus eos* — Cone 1980, New Brunswick; *Culaea inconstans* — Dechtiar 1972b, Ontario; *Cymatogaster aggregata* — Arai 1969, Pacific; *Etheostoma exile* — Dechtiar 1972c, Ontario, Lubinsky and Loch 1979, Manitoba; *E. nigrum* — Dechtiar 1972c, Ontario, Lubinsky and Loch 1979, Manitoba; *Fundulus heteroclitus* — Gowanloch 1927, Atlantic; *Gadus morhua* — Appy and Burt 1982, Atlantic; *Hybognathus hankinsoni* — Molnar et al. 1974, Ontario; *Micropterus dolomieui*[64] — Cooper 1915, Ontario; *Moxostoma anisurum, M. macrolepidotum* — Dechtiar 1972b, Ontario; *Nocomis biguttatus* — Molnar et al. 1974, Ontario; *Notropis anogenus* — Dechtiar 1972c, Ontario, Lubinsky and Loch 1979, Manitoba; *N. cornutus* — Molnar et al. 1974, Ontario; *N. hudsonius* — Dechtiar 1972b, Ontario; *Noturus gyrinus* — Dechtiar 1972c, Ontario, Lubinsky and Loch 1979, Manitoba; *Oncorhynchus nerka* — Bell and Margolis 1976, British Columbia; *Percopsis omiscomaycus* — Dechtiar 1972c, Ontario, Lubinsky and Loch 1979, Manitoba; *Pungitius pungitius* — Leong and Holmes 1981, Alberta; *Salmo clarki* — Hoskins et al. 1976, British Columbia; *S. gairdneri* — Hare and Frantsi 1974, Nova Scotia, Hoskins and Hulstein 1977, British Columbia; *S. salar* — Hare and Frantsi 1974, Nova Scotia, Hare and Burt 1975a, 1975b, New Brunswick; *Salvelinus fontinalis* — Hicks and Threlfall 1973, Labrador, Hare and Frantsi 1974, Nova Scotia; *Semotilus atromaculatus* — Cone 1980, New Brunswick.

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[64] See footnote 61.

Laminiscus Pálsson and Beverley-Burton, 1983 (Fig. 37:0)

Gyrodactylidae: body elongate. Marginal hooks with relatively short, straight shaft and distributed in three groups on periphery of haptor: two anterolateral groups of four hooks each and one posterior group of eight, more widely distributed hooks. Hamuli with short deep root and elongate superficial root. One connecting transverse bar present and thin, sclerotized plate extending from distal end of superficial roots to bar, supporting hamuli and anterolateral groups of marginal hooks. Haptoral suction disc absent. On gills of marine and brackish water teleosts.

37:0

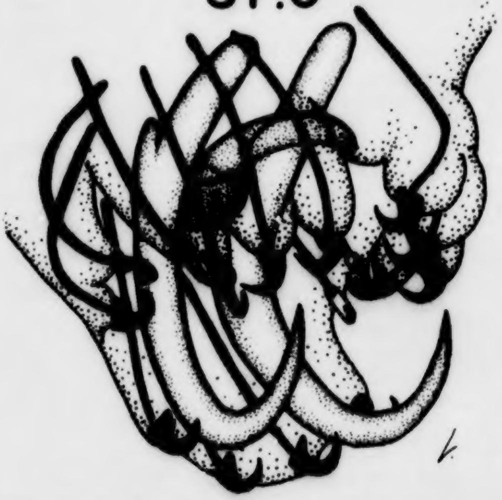

FIG. 37:0. *Laminiscus* — haptoral characters (based on Pálsson and Beverley-Burton 1983).

Key to species of *Laminiscus*

1 Superficial and deep roots of hamuli form an angle of approximately 90° at point of fusion. On osmerids ....

.. *L. gussevi* (Bykhovsky and Polyansky, 1953) Pálsson and Beverley-Burton, 1983 (Fig. 37:1, Table 21)
On gills of *Mallotus villosus*
Record: Pálsson and Beverley-Burton 1983 (Atl)

Superficial and deep roots of hamuli form an acute angle (less than 90°) at point of fusion. On salmonids ....

L. strelkowi (Bykhovsky and Polyansky, 1953) Pálsson and Beverley-Burton, 1983 (Fig. 37:2, Table 21)
On gills of *Oncorhynchus gorbuscha, O. nerka*
Record: Margolis 1956 (Pac, BC-b)

Records of unidentified Gyrodactylidae gen. spp. are listed from:

Catostomus commersoni, Chrosomus neogaeus, Ictalurus nebulosus, Lepomis gibbosus, Micropterus dolomieui, Notropis cornutus, N. heterolepis, Perca flavescens, Semotilus atromaculatus — Bangham 1941, Ontario.

Note: Part of the material recorded as Gyrodactylidae by Bangham (1941) was later identified to species by Mizelle and Donahue (1944).

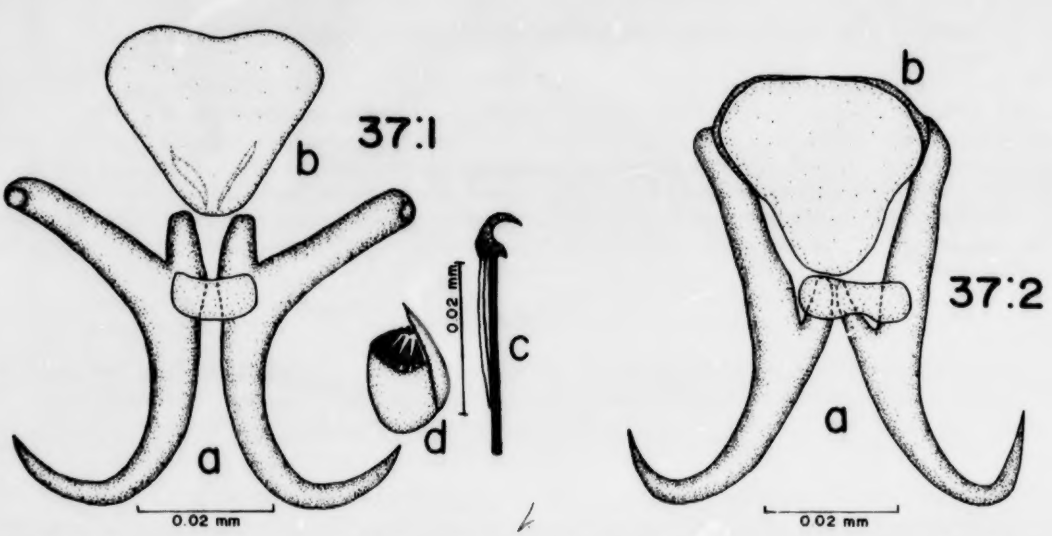

FIG. 37:1–37:2. *Laminiscus* spp. 37:1. *L. gussevi* (redrawn from Pálsson and Beverley-Burton 1983): a. hamuli and transverse bar; b. sclerotized plate; c. marginal hook; d. penis. 37:2. *L. strelkowi* (redrawn from Bykhovsky and Polyansky 1953): a. hamuli and transverse bar; b. sclerotized plate.

Records of unidentified Gyrodactyloidea[65] gen. spp. are listed from:

Acrocheilus alutaceus — Bangham and Adams 1954, British Columbia; *Ambloplites rupestris* — Bangham 1955, Ontario; *Ammodytes hexapterus* — Arai 1967, 1969, Pacific; *Catostomus catostomus, C. macrocheilus* — Bangham and Adams 1954, British Columbia; *Chrosomus eos* — Bangham 1955, Ontario; *Clupea harengus pallasi* — Arai 1967, 1969, Pacific; *Cottus asper, C. cognatus, C. rhotheus, Couesius plumbeus, Culaea inconstans* — Bangham and Adams 1954, British Columbia; *C. inconstans* — Bangham 1955, Ontario; *Cymatogaster aggregata* — Arai 1967, 1969, Pacific; *Cyprinus carpio* — Bangham and Adams 1954, British Columbia; *Esox lucius, E. masquinongy, Etheostoma nigrum* — Bangham 1955, Ontario; *Gasterosteus aculeatus* — Bangham and Adams, 1954, British Columbia, Arai 1967, Pacific; *Ictalurus nebulosus* — Bangham and Adams 1954, British Columbia, Bangham 1955, Ontario; *I. punctatus* — Bangham and Hunter 1939, Ontario, Bangham 1955, Ontario; *Lepomis gibbosus* — Bangham and Adams 1954, British Columbia, Bangham 1955, Ontario; *L. macrochirus* — Bangham and Hunter 1939, Ontario; *Micropterus dolomieui* — Bangham and Hunter 1939, Ontario, Bangham 1955, Ontario; *M. salmoides* — Bangham and Hunter 1939, Ontario, Bangham and Adams 1954, British Columbia, Bangham 1955, Ontario; *Morone chrysops* — Bangham and Hunter 1939, Ontario, Bangham 1955, Ontario; *Mylocheilus caurinus* — Bangham and Adams 1954, British Columbia, Anon. 1978, British Columbia, Arai and Mudry 1983, British Columbia; *Notemigonus crysoleucas, Notropis antherinoides, N. cornutus, N. heterolepis, N. hudsonius* — Bangham 1955, Ontario; *Oligocottus maculosus* — Arai 1969, Pacific; *Oncorhynchus kisutch* — Bangham and Adams 1954, British Columbia, Arai 1967, 1969, Pacific; *Perca flavescens, Percina caprodes, Percopsis omiscomaycus* — Bangham 1955, Ontario; *Pholis ornata* — Arai 1967, 1969, Pacific; *Pimephales notatus* — Bangham 1955, Ontario; *Platichthys stellatus* — Arai 1967, 1969, Pacific; *Pomoxis nigromaculatus* — Bangham and Adams 1954, British Columbia, Bangham 1955, Ontario; *Prosopium williamsoni* — Bangham and Adams 1954, British Columbia, Anon. 1978, British Columbia, Arai and Mudry 1983, British Columbia; *Ptychocheilus oregonensis* — Bangham and Adams 1954, British Columbia, Anon. 1978, British Columbia, Arai and Mudry 1983, British Columbia; *Rhinichthys cataractae, Richardsonius balteatus, Salmo clarki, Salvelinus malma* — Bangham and Adams 1954, British Columbia; *Semotilus atromaculatus, Stizostedion vitreum vitreum* — Bangham 1955, Ontario; *Syngnathus griseolineatus* — Arai 1967, 1969, Pacific; *Thymallus arcticus* — Bangham and Adams 1954, British Columbia.

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[65] The designation "Gyrodactyloidea" used by Bangham and Adams (1954) was sensu Dawes (1946) (Adams 1984, pers. comm.), which included dactylogyrids as well as gyrodactylids. Thus, some of the "Gyrodactyloidea" of Bangham and Adams (1954) were identified as various *Dactylogyrus* spp. by Monaco and Mizelle (1955).

ORDER POLYOPISTHOCOTYLIDA (Odhner, 1912, suborder) status emend.

Haptor of adult complex, often subdivided, with paired[66] muscular "sucker-like attachment organs"[67] or clamps replacing marginal hooks of larval haptor immediately anterior to hamuli (i.e. III, IV, V and VI). Larval haptor with (primitively) 16 marginal hooks which may be secondarily reduced to 14, 12, or 10; posteriormost pair (I) not migrating anteriorly but remaining peripheral so that two pairs (I and II) lie between hamuli.[68] Primitively, two pairs of eyes (with lenses) present. Blood feeders, mouth either surrounded by oral sucker, or with pair of buccal suckers inside oral cavity, or with pair of anterior, sucker-like depressions, not connected with buccal cavity; genito-intestinal canal present. Oviparous. Marine, freshwater, and brackish water.

Key to superfamilies of Polyopisthocotylida[69]

1 Haptor with three pairs large, muscular suckers and tapering posteriorly to form terminal appendix with (usually) one pair of smaller suckers (Fig. 38:0). Each large sucker surrounds single median (keratinized) sucker sclerite,[70] peripheral (nonkeratinized) sclerites lacking. Parasites of elasmobranchs or Acipenseriformes 2

Haptor with four pairs (Fig. 46:0) or numerous (Fig. 53:0) clamps comprising median sclerites(s) (nonkeratinized) and peripheral (nonkeratinized) sclerites. Parasites of teleosts .... Mazocraeoidea

2 Parasites of Acipenseriformes. Terminal appendix of haptor short, with or without rudimentary suckers (Fig. 38:0), three pairs of well-developed hook-like sclerites[71] present (Fig. 38:1). Eyes (two pairs) present .... Diclybothrioidea

Parasites of elasmobranchs. Terminal appendix of haptor elongate, with one pair unarmed suckers (Fig. 40:0), one pair hamuli and one pair minute marginal hooks[72] present (Fig. 40:1). Eyes lacking .... Hexabothrioidea

DICLYBOTHRIOIDEA (Bykhovsky, 1957 order[73]) status emend.

Polyopisthocotylida: larval haptor lacking marginal hooks VII and VIII. Adult haptor with three pairs suckers, each supported by median (keratinized) sucker sclerite developed near marginal hooks IV, V, and VI; terminal haptoral appendix short, with or without rudimentary suckers, three pairs of well-developed sclerites[74] present. Two pairs of eyes. Mouth flanked by two muscular, ventral depressions, not connected with buccal cavity. Freshwater and brackish water, on teleosts.

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[66] Unpaired/asymmetrical in some taxa which have multiple clamps. e.g. Heteraxinidae and Microcotylidae.

[67] Hereafter referred to as "suckers".

[68] Except in the Hexabothrioidea in which the larval haptor lacks pair I.

[69] The taxa represented in this section have (according to Llewellyn, 1970) evolved from a branch in which marginal hook pairs VII and VIII were lacking; pairs III, IV, V, and VI were surrounded by suckers or clamps; pairs II and I lay between the single pair of hamuli with I being enlarged and lacking a domus.

[70] Terminology of Lyons (1966) who considered these structures, which support the adhesive organs of "hexabothriids, diclybothriids and chimaericolids", to be adult organs and not of larval origin. In the "hexabothriids" they are formed near the site of the larval marginal hooks.

[71] The terminology and homology of these sclerites are confused. At least one pair may be homologous with the "sucker sclerites" of Lyons (1966). Wright and Dechtiar (1974) noted that two of the three pairs of "hooks" are large and C-shaped and the third pair is smaller and straight.

[72] In the Hexabothrioidea the larva has only five pairs of marginal hooks (i.e. pairs I, VII, and VIII are lacking). Thus, the terminal appendix of the adult carries pair II which lie between the hamuli (Llewellyn 1970; Wiskin 1970).

[73] As Diclybothriidea.

[74] See footnote 71.

DICLYBOTHRIIDAE Bykhovsky and Gusev, 1950

Diclybothrioidea: caeca diverticulate, confluent posteriorly, with posterior diverticulum extending into haptor or not. Testes numerous, postovarian. Vaginae paired. Eggs without filaments. On gills of Acipenseriformes.

Key to genera of Diclybothriidae

1 Haptoral appendix well developed, with suckers; largest appendicular sclerites almost equal in size to haptoral sucker sclerites .... *Diclybothrium*

Haptoral appendix rudimentary, without suckers; none of appendicular sclerites even 2/3 as long as haptoral sucker sclerites .... *Paradiclybothrium*

Diclybothrium Leuckart, 1835 (Fig. 38:0)

Diclybothriidae: haptoral appendix well developed, protruding posteriorly beyond haptoral margin, with rudimentary suckers;[75] largest (of three pairs) of appendicular sclerites almost as long as haptoral sucker sclerites. Posterior caecal diverticulum extending to middle or posterior region of haptor. On gills of *Acipenser* spp.

Key to species of *Diclybothrium*

1 Testes "very numerous" — 300 or more; eggs distinctly oval, 0.21–0.22 mm long .... *D. armatum* Leuckart, 1835 (Fig. 38:1)

Morphometric data (from Price 1942): total body length 2.50–13.00 mm, width 0.23–1.10 mm; haptor length 0.32–1.00 mm, width 0.32–0.80 mm; haptoral suckers 0.20–0.37 mm diameter, sucker sclerites 0.40–0.47 mm long; appendicular sclerites (length) — outer 0.44–0.54 mm, middle 0.34–0.35 mm, inner 0.10–0.12 mm. Testes number 300 or more. Eggs 0.21–0.22 mm long and 0.09–0.14 mm wide.

On gills of *Acipenser brevirostrum* (5); *A. fulvescens* (1,2,3,4,6)

Records: 1. Stafford 1904 (Ont); 2. Cooper 1915 (Ont); 3. Dechtiar 1972b (Ont); 4. Anthony 1974 (Ont); 5. Appy and Dadswell 1978 (NB); 6. Lubinsky and Loch 1979 (Man)

Testes "about" 150; eggs ovoid or rounded, 0.08–0.16 mm long .... *D. hamulatum* (Simer, 1929) Price, 1942 (Fig. 38:2)

Morphometric data (from Simer 1929): total body length 1.22–8.44 mm. Testes number "about 150". Eggs 0.08–0.16 mm long. Price (1942) considered the haptoral sclerotizations of *D. hamulatum* to be "more robust" than those of *D. armatum* but did not provide measurements.

On gills of *Acipenser fulvescens*

Record: Bangham 1955 (Ont)

Paradiclybothrium Bykhovsky and Gusev, 1950 (Fig. 39:0, 39:1)

Diclybothriidae: haptoral appendix rudimentary, only protruding slightly beyond haptoral margin, lacking suckers; largest (of three pairs) of appendicular sclerites not even as long as 2/3 of haptoral sucker sclerites. Posterior caecal diverticulum not extending into haptoral region. On gills of *Acipenser* sp.

Record of an unidentified *Paradiclybothrium* sp. is listed from:

Acipenser fulvescens — Anthony 1974, Ontario.

Remarks: Anthony (1974) stated this material was "probably" *Paradiclybothrium* sp. The genus contains a single species, *P. pacificum* Bykhovsky and Gusev, 1950, found on *A. medirostris* taken in estuarine waters of the eastern USSR. Further studies on Canadian material are necessary to make a precise identification.

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[75] Wright and Dechtiar (1974) did not see rudimentary suckers in *D. armatum* although they were visible in stained specimens of this species made available to me by Dr R. Appy.

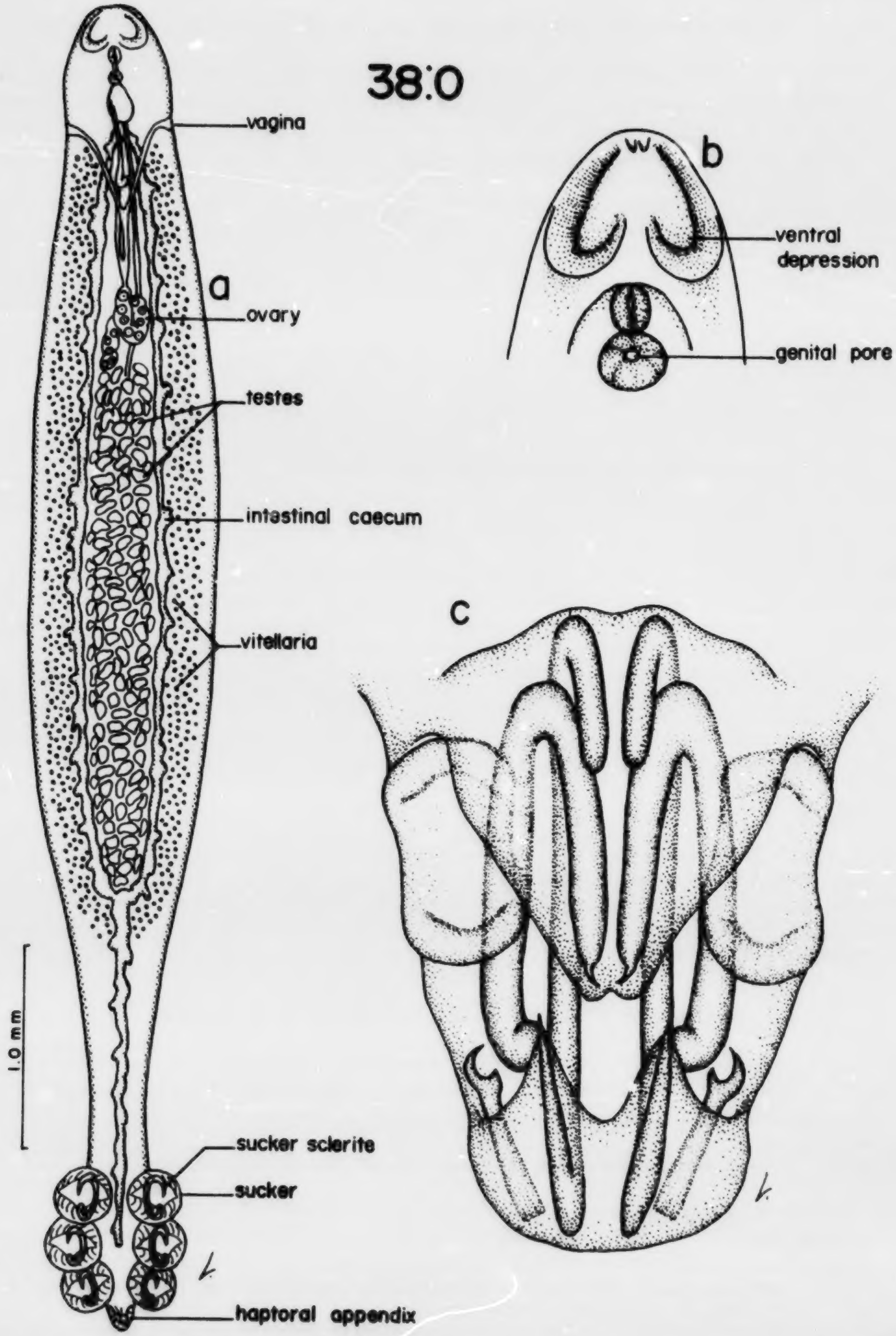
38:0
a
vagina
ovary
testes
intestinal caecum
vitellaria
1.0 mm
sucker sclerite
sucker
haptoral appendix
b
ventral depression
genital pore
c

FIG. 38:0. *Diclybothrium* — generic characters (modified from Bykhovsky and Gusev 1950 with original observations): a. whole animal, ventral view; b. anterior region, ventral view; c. haptoral appendix with rudimentary suckers and appendicular sclerites.

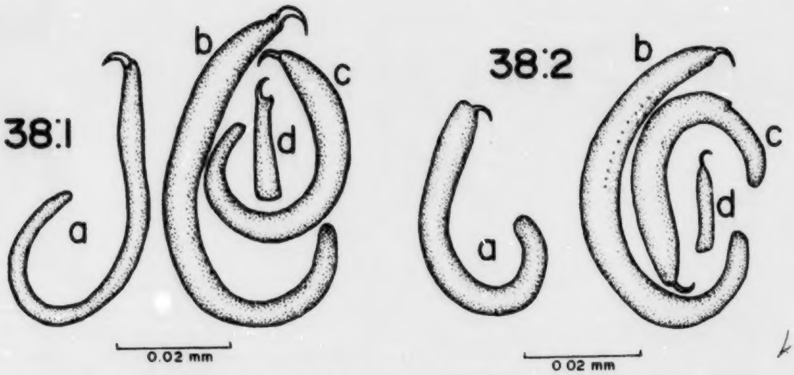

FIG. 38:1–38:2. *Diclybothrium* spp. 38:1. *D. armatum* (redrawn from Price 1942): a. haptoral sucker sclerite; b. outer appendicular sclerite; c. median appendicular sclerite; d. inner appendicular sclerite. 38:2. *D. hamulatum* (redrawn from Price 1942): a. haptoral sucker sclerite; b. outer appendicular sclerite; c. median appendicular sclerite; d. inner appendicular sclerite.

HEXABOTHRIOIDEA (="hexabothriid" sensu Llewellyn, 1970) status emend.

Polyopisthocotylida: larval haptor lacking marginal hooks I,[76] VII and VIII. Adult body elongate, haptor with three pairs suckers, each supported by median (keratinized) sucker sclerite developed near marginal hooks IV, V and VI; terminal haptoral appendix with one pair unarmed suckers and one pair hamuli between which lie marginal hooks II.[76] Eyes lacking. Mouth apparently surrounded by circumoral sucker. Marine, on elasmobranchs.[77]

HEXABOTHRIIDAE Price, 1942[78]

Hexabothrioidea: haptor symmetrical or asymmetrical. Caeca diverticulate, confluent posteriorly, posterior diverticulum extending into haptor. Testes numerous, postovarian; penis unarmed or (more rarely) armed. Vaginae paired, either parallel (not confluent before entering transverse vitelline duct) or forming V or Y (confluent before entering transverse vitelline duct). Eggs with or without filament(s). On Rajidae, Scyliorhinidae, and Squalidae.

Key to genera of Hexabothriidae

1 Vaginae confluent before entering transverse vitelline duct (Y); eggs lacking polar filaments, shell with longitudinal ridges. Parasites of Rajidae and Scyliorhinidae .... *Rajonchocotyle*

Vaginae not confluent before entering transverse vitelline duct; eggs with two polar filaments, shell without longitudinal ridges. Parasites of Squalidae .... *Squalonchocotyle*

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[76] See Wiskin (1970).

[77] According to Euzet and Maillard (1974) *Squalonchocotyle callorhynchi* Manter, 1955 was described from material found on the gills of a holocephalan.

[78] The majority of characters included in this diagnosis are those listed by Euzet and Maillard (1974) as being important for the separation of hexabothriid genera.

39:0

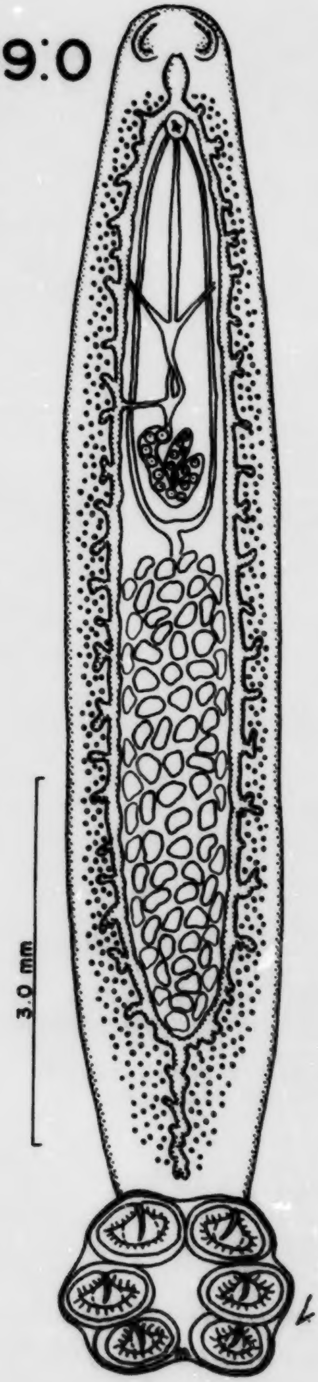

FIG. 39:0. *Paradiclybothrium* — generic characters (modified from Bykhovsky and Gusev 1950): whole animal, ventral view.

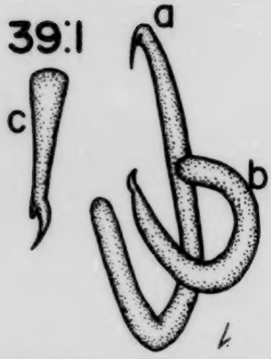

FIG. 39:1. *Paradiclybothrium* sp. (redrawn from Bykhovsky and Gusev 1950): a. outer appendicular sclerite; b. median appendicular sclerite; c. inner appendicular sclerite.

Rajonchocotyle Cerfontaine, 1899[79] (Fig. 40:0)

Hexabothriidae: penis unarmed. Vaginae confluent before entering transverse vitelline duct (forming Y); seminal receptacle sac-like; ootype wall with longitudinal striations; eggs lacking polar filaments but with seven longitudinal ridges. On gills of Rajidae and Scyliorhinidae. One species on Canadian fishes.

Rajonchocotyle emarginata (Olsson, 1876) Sproston, 1946 (Fig. 40:1)

Descriptive and morphometric data (from Price 1940): body length, excluding haptoral appendix, 5 mm,[80] by 1.8 mm; haptor 2.5 mm wide, appendix 1.36 mm long, haptoral suckers about 595 in diameter, sucker sclerites, total (axial) length about 1140; eggs 170–197 by 80 to 97.

On gills of *Raja radiata*
Record: Redkozubova 1976 (Atl)

Squalonchocotyle Cerfontaine, 1899[81] (Fig. 41:0)

Hexabothriidae: penis unarmed. Vaginae parallel, not confluent before entering transverse vitelline duct; seminal receptacle sac-like; ootype wall with longitudinal striations; eggs with two polar filaments. On gills of Squalidae. One species on Canadian fishes.

Squalonchocotyle abbreviata (Olsson, 1876) Cerfontaine, 1899 (Fig. 41:1)

Descriptive and morphometric data (from Bonham 1950): body length, excluding haptoral appendix, 2–8 mm, by 1.25–1.5 mm; sucker sclerites, total (axial) length 668 (561–775); testes 38 in number; eggs 260 by 130, usually with two short polar filaments.

On gills of *Squalus acanthias*
Records: Stafford 1904 (Atl); 1907 (Atl); Threlfall 1969 (Atl)

MAZOCRAEOIDEA (Bykhovsky, 1957 order)[82] status emend.

Polyopisthocotylida: larval haptor lacking marginal hooks VII and VIII. Adult haptor with four pairs (developed near marginal hooks III, IV, V and VI) or many, clamps.[83] Each clamp with complex sclerotized framework comprising anterior and posterior jaws made up of peripheral (nonkeratinized) sclerites, and median

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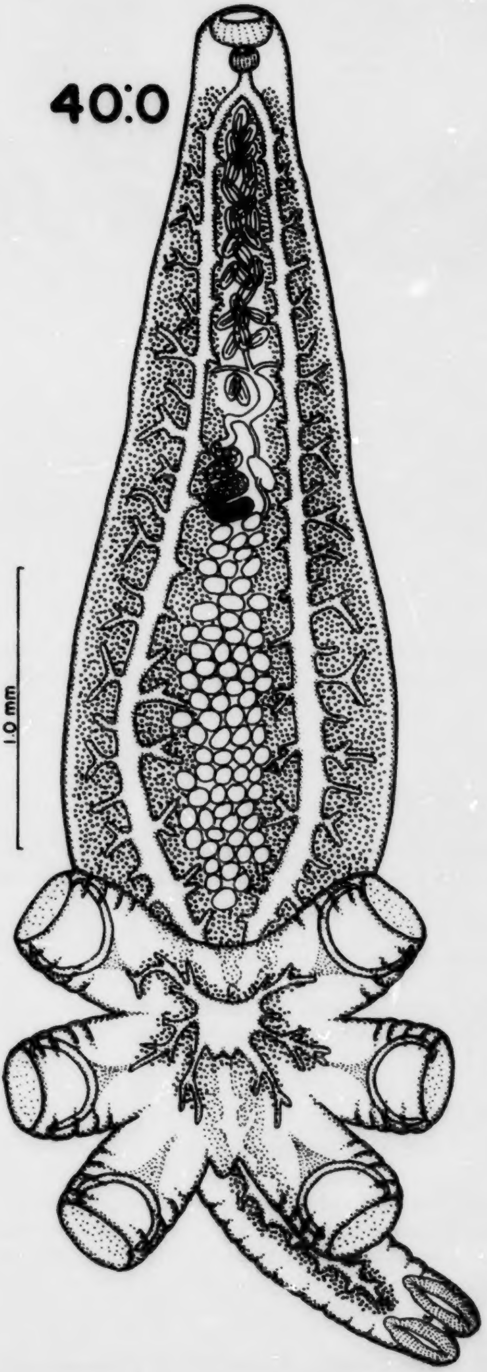
[79] Diagnosis based on characters listed by Euzet and Maillard (1974).

[80] Price (1940) stated "body proper" 5 mm long.

[81] Diagnosis based on characters listed by Euzet and Maillard (1974).

[82] As Mazocraeidea, which is not taxonomically equivalent in the present context. However, see Llewellyn's (1970) "mazocraeidea" of unstated rank which *is* comparable.

[83] The term "clamp" is used for the mazocraeoidean attachment organs although, according to Llewellyn (1958), attachment in *Diclidophora* spp. involves suction rather than a clamping device.



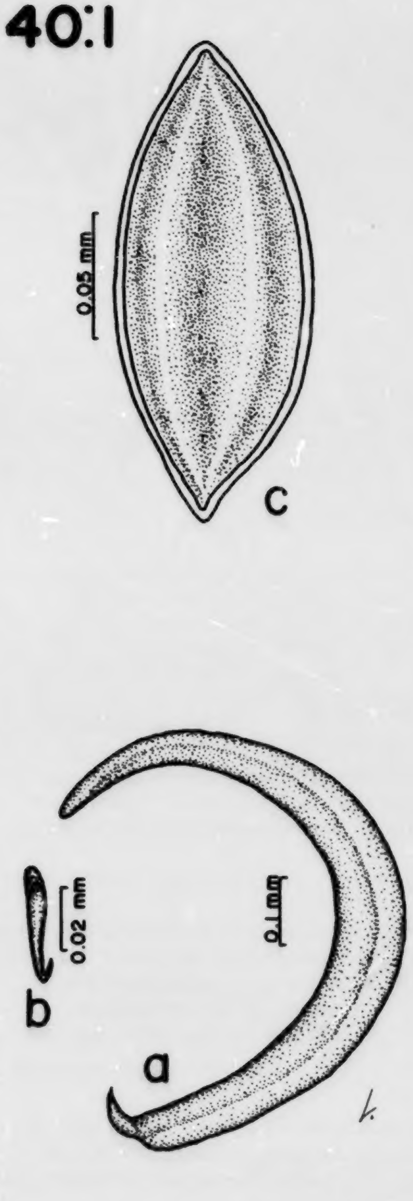

40:1
0.05 mm
c
0.02 mm
b
0.1 mm
a

FIG. 40:0. *Rajonchocotyle* — generic characters (based on Price 1940): whole animal, ventral view.

FIG. 40:1. *Rajonchocotyle emarginata* (redrawn from Price 1940): a. haptoral sucker sclerite; b. hamulus; c. egg.

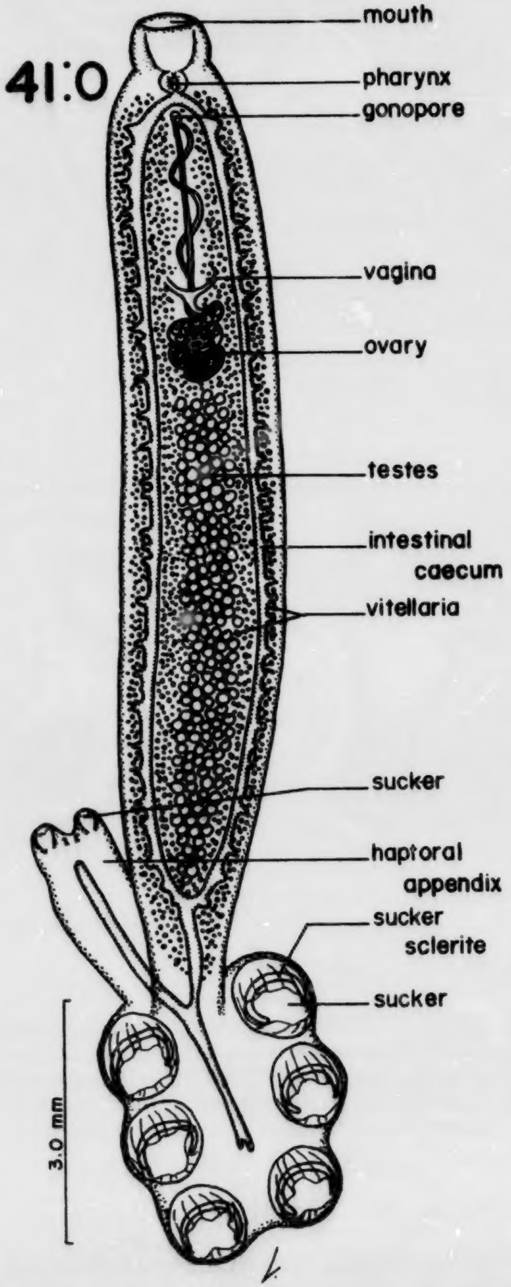

41:0
mouth
pharynx
gonopore
vagina
ovary
testes
intestinal caecum
vitellaria
sucker
haptoral appendix
sucker sclerite
sucker
3.0 mm

FIG. 41:0. *Squalonchocotyle* — generic characters (modified from Bonham 1950 with original observations): whole animal, ventral view.

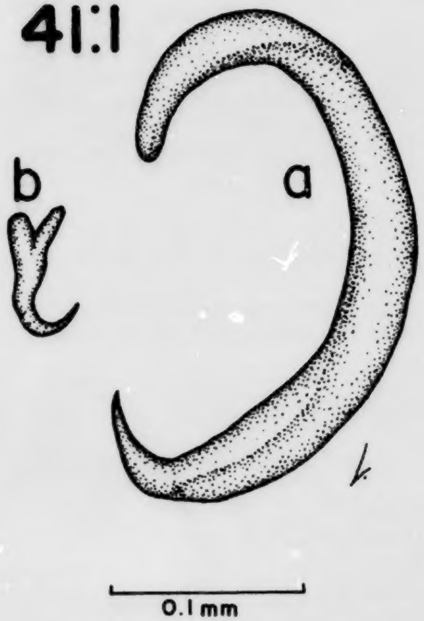


FIG. 41:1. *Squalonchocotyle abbreviata* (redrawn from Sproston 1946): a. haptoral sucker sclerite; b. hamulus.

(nonkeratinized) sclerite(s).[84] One pair hamuli (if present) on posterior border of haptor with marginal hooks I and II (if present) lying between; pair I (if present) enlarged. Eyes present or degenerate. Mouth with pair of buccal suckers inside oral cavity. Marine and freshwater, on teleosts.

Key to families of Mazocraeoidea

1 Four pairs clamps arranged symmetrically (Fig. 44:0) 2

Numerous clamps arranged symmetrically (Fig. 53:1) or asymmetrically (Fig. 49:0) 5

2 Central sclerites of clamps modified to form "fair-lead" system (Fig. 50:1).[85] Genital bulb with two longitudinal rows of hooks and pair armed anterolateral processes (Fig. 50:1) ..... Mazocraeidae

Central sclerite(s) of clamps not modified to form "fair-lead" system (Fig. 42:2, 44:1, 46:1). Genital pore unarmed or with genital corona (Fig. 42:1, 44:0) 3

3 Haptoral clamps pedunculate, asymmetrical (Fig. 44:1) .... Diclidophoridae

Haptoral clamps sessile, symmetrical (Fig. 42:1, 46:1) 4

4 Anterior haptoral clamps conspicuously large; posterior three pairs small, situated on haptoral extension; terminal lappet on posterior margin of extension, with one pair of hamuli and two pairs of marginal hooks (Fig. 42:0) .... Anthocotylidae

Anterior haptoral clamps not (or only slightly) larger than others; terminal lappet lacking (Fig. 46:0) .... Discocotylidae

5 Haptor bilaterally symmetrical; clamps, more or less equally distributed on lateral margins (Fig. 53:0) .... Microcotylidae

Haptor asymmetrical; clamps not equally distributed on lateral margins (Fig. 49:0) .... Heteraxinidae

ANTHOCOTYLIDAE Bykhovsky, 1957

Mazocreaoidea: haptor symmetrical with four pairs sessile, symmetrical, clamps; anterior pair conspicuously large, posterior three pairs small, lying on narrow, posterior haptoral extension; terminal lappet with one pair hamuli flanking two pairs marginal hooks of which pair I is enlarged. Caeca with internal and external diverticula, not confluent posteriorly but extending to haptoral prolongation. Testes numerous, follicular, postovarian; penis with ring of sclerotized hooks. Vaginae paired. Marine, on Gadidae. One genus, *Anthocotyle*, on Canadian fishes.

Anthocotyle van Beneden and Hesse, 1863 (Fig. 42:0)

Anthocotylidae: haptor basically symmetrical (unequal development of right and left clamps of anterior pair may occur). Vaginal pores submarginal, at level of genital pore, vaginae opening into longitudinal vitelline ducts; vitellaria coextensive with intestinal caeca from level of genital pore to prehaptoral peduncle. On gills of Gadidae. One species on Canadian fishes.

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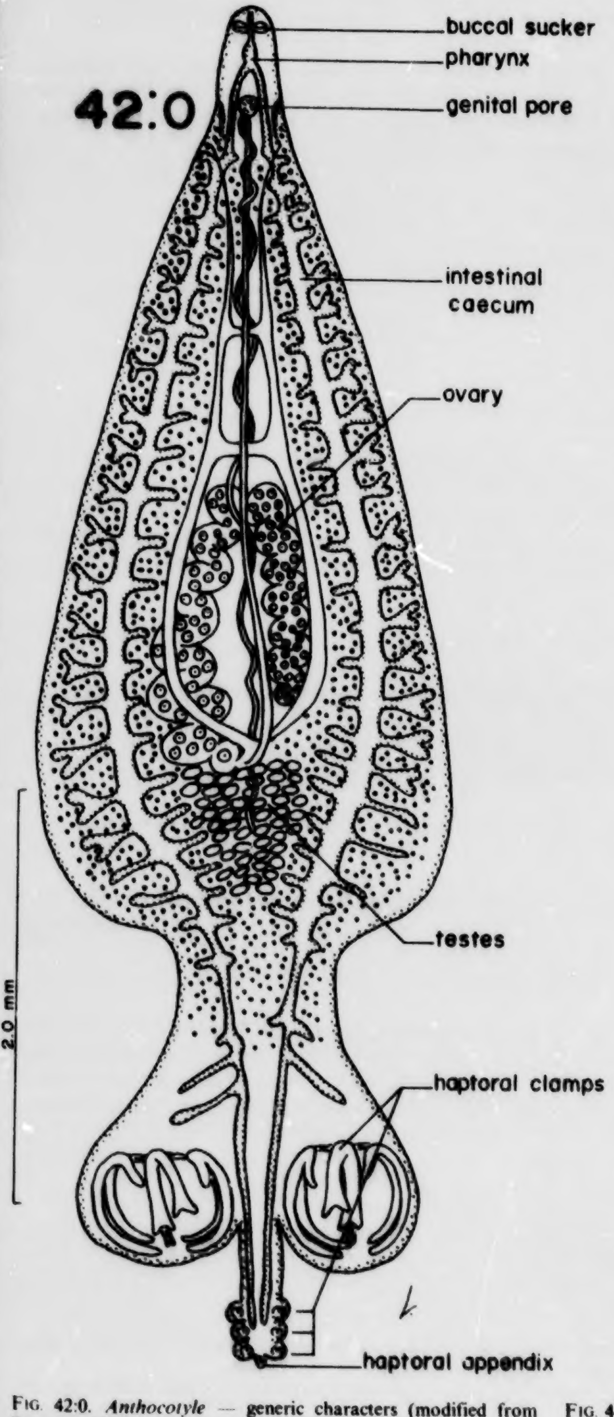
[84] See Lyons (1966) and Llewellyn (1970) — this sclerite is not considered to be homologous with that of the Hexabothrioidea and Diclybothrioidea which is keratinized, but is regarded as a differently developed structure, of similar composition as the peripheral sclerites. A secondary reduction of peripheral and median sclerites is evident in some taxa.

[85] See Llewellyn (1957).

42:0


buccal sucker
pharynx
genital pore
intestinal caecum
ovary
testes
haptoral clamps
haptoral appendix
2.0 mm

42:1

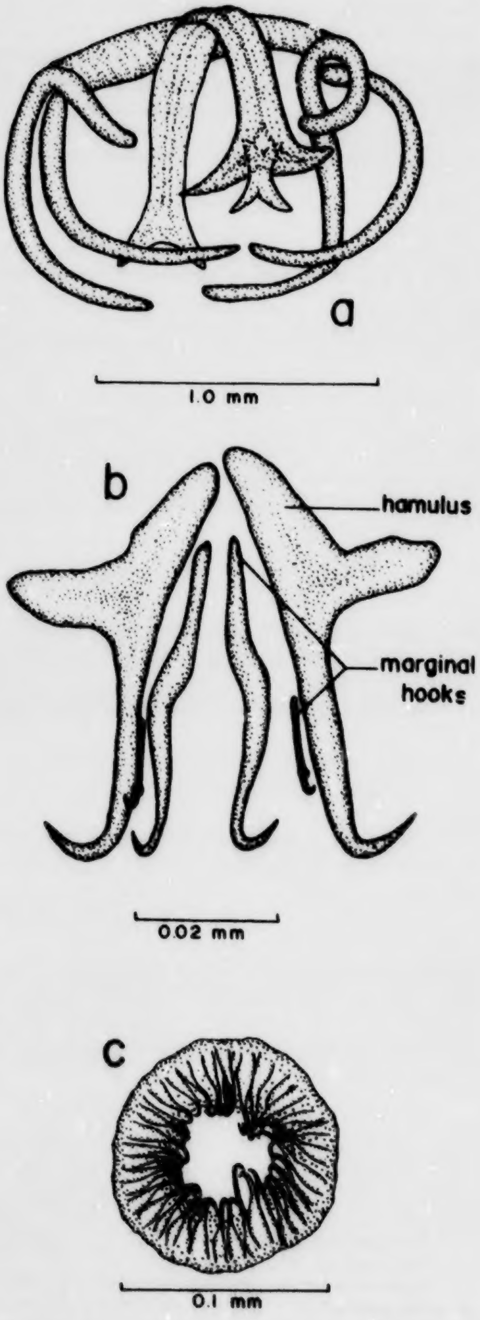

a
1.0 mm
b
hamulus
marginal hooks
0.02 mm
c
0.1 mm

FIG. 42:0. *Anthocotyle* — generic characters (modified from Sproston 1946): whole animal, ventral view.

FIG. 42:1. *Anthocotyle merluccii* (modified from Sproston 1946 and Price 1943b): a. haptoral clamp; b. hamuli and marginal hooks; c. genital corona.

Anthocotyle merluccii van Beneden and Hesse, 1863, (Fig. 42:1)

Descriptive and morphometric data (from Price 1943b): body 6.0–6.9 mm long by 1.1 mm wide; anterior haptoral clamps unequal in size (right 0.94–1.20 mm wide, left 0.68–0.85 mm wide), those of posterior three pairs equal in size (0.07–0.09 mm wide), hamuli 60 long, marginal hooks — pair I 45 long, pair II 20 long. Penile spines 35–38 in number, measuring 0.03 mm long.

On gills of *Merluccius bilinearis*

Records: Stafford 1904 (Atl); 1907 (Atl)

Remarks: Originally described from worms found on the gills of *Merluccius vulgaris* taken off the coast of Belgium, *A. merluccii* has since been reported from *Merluccius* spp. from both the eastern and western North Atlantic. MacCallum (1916) proposed a subspecies, *A. merluccii americanus*, which was designated *A. americanus* by Price (1943b). However, Sproston (1946), Dawes (1946), and Brinkmann (1952) considered *A. americanus* to be identical with *A. merluccii*. Crane (1972) erroneously reported MacCallum's (1916) record from *M. bilinearis* as being from Canadian waters. The correct locality is Woods Hole, Mass., U.S.A.

DICLIDOPHORIDAE Fuhrmann, 1928

Mazocraeoidea: haptor symmetrical with four pairs asymmetrical clamps; both anterior and posterior jaws of clamps with inner and outer compartments; suctional diaphragm[86] or adhesive (?) callous[87] may or may not be incorporated in at least some clamps. Posterior border of haptor with one or two pairs hooks.[88] Intestinal caeca with internal and external diverticula; confluent or not confluent posteriorly, extending into posterior region of haptor. Genital pore with corona armed with circle of spines or (more rarely) unarmed. Marine, on Gadiformes.

Key to genera of Diclidophoridae

1 Haptor bilobed, each lobe with four pedunculate clamps. At least one of second and third pairs of clamps with adhesive callous.[89] On gills of *Macrourus* spp. .... *Macruricotyle*

Haptor not bilobed. Clamps without adhesive callous 2

2 Haptor deeply divided with eight elongate, slender peduncles. Genital pore with unarmed corona. On gills of *Macrourus* spp .... *Cyclocotyloides*

Haptor not deeply divided, peduncles, if present, short and stout. Genital pore with armed corona. On gills of Gadidae .... *Diclidophora*

Cyclocotyloides Price, 1943 (Fig. 43:0)

Diclidophoridae: body elongate, narrowing anteriorly, clearly separate from haptor. Haptor deeply divided into eight distinct peduncles each with single clamp, terminal lappet (in immature specimens) with one pair minute hooks.[90] Intestinal caeca confluent posteriorly. Testes numerous, postovarian; genital corona unarmed. Ovary looping; vitellaria extending into haptoral region. On gills of Macrouridae. One species on Canadian fishes.

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[86] See Llewellyn (1958).

[87] See Campbell et al. (1982).

[88] According to Price (1943a) *Diclidophora maccallumi* has two pairs of hooks: it is probable these are a pair of hamuli and one pair (I) of marginal hooks — they may have been either overlooked or be secondarily reduced in other species.

[89] Right clamp of third pair in *M. clavipes* (see Mamaev and Lyadov 1975) and both clamps of second and third pairs in *M. newfoundlandae* (see Campbell et al. 1982).

[90] See McCauley and Smoker (1969).

43:0

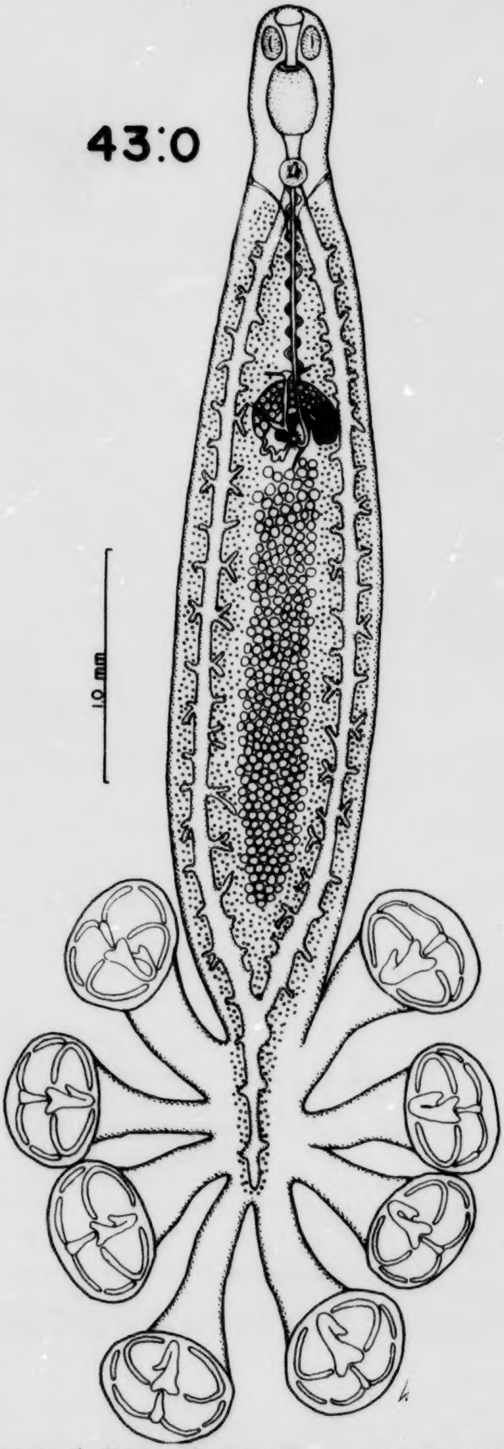


FIG. 43:0. *Cyclocotyloides* — generic characters (based on Mamaev and Lyadov 1975): whole animal, ventral view.

43:1

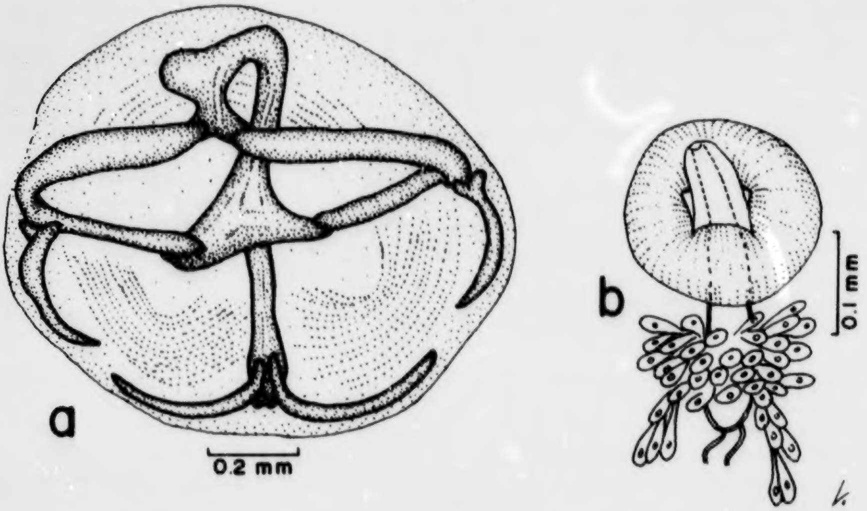


FIG. 43:1. *Cyclocotyloides pinguis* (redrawn from Mamaev and Lyadov 1975): a. haptoral clamp; b. penis.

Cyclocotyloides pinguis (Linton, 1940) Price, 1943 (Fig. 43:1)

Descriptive and morphometric data (from McCauley and Smoker 1969): body (excluding haptor) 2.75–5.00 mm by 0.95–2.15 mm maximum (midbody) width. Buccal suckers 0.15 mm by 0.30 mm; penis 0.12–0.21 mm diameter.

On gills of *Macrourus berglax*
Record: Zubchenko 1981 (Atl)

Diclidophora Diesing, 1850 (Fig. 44:0)

Diclidophoridae: body markedly tapering anteriorly, merging into haptoral region posteriorly. Intestinal caeca, not confluent posteriorly, extending into clamp peduncles. Testes numerous, postovarian; genital corona armed with spines. Ovary looping; vitellaria extending into haptoral region. On gills of Gadiformes, typically (but not exclusively) Gadidae.

Key to species of *Diclidophora*

1 Haptoral clamps each with denticulate patch on outer surface of outer compartment of anterior jaw .... *D. denticulata* (Olsson, 1876) Price, 1943 (Fig. 44:1)

Descriptive and morphometric data (from Price 1943a): body 7 mm long by 1.6 mm maximum (midbody) width; haptor 2.1 mm long, clamps 0.68 mm wide, denticulate patch with 30–40 spines; penis 0.1 mm diameter, corona with 13 spines.

On gills of *Pollachius virens*
Records: Stafford 1904 (Atl); 1907 (Atl); Cooper 1915 (Atl); Appy 1983 (pers. comm.) (Atl)

Haptoral clamps lacking denticulate patch on outer surface of outer compartment of anterior jaw 2

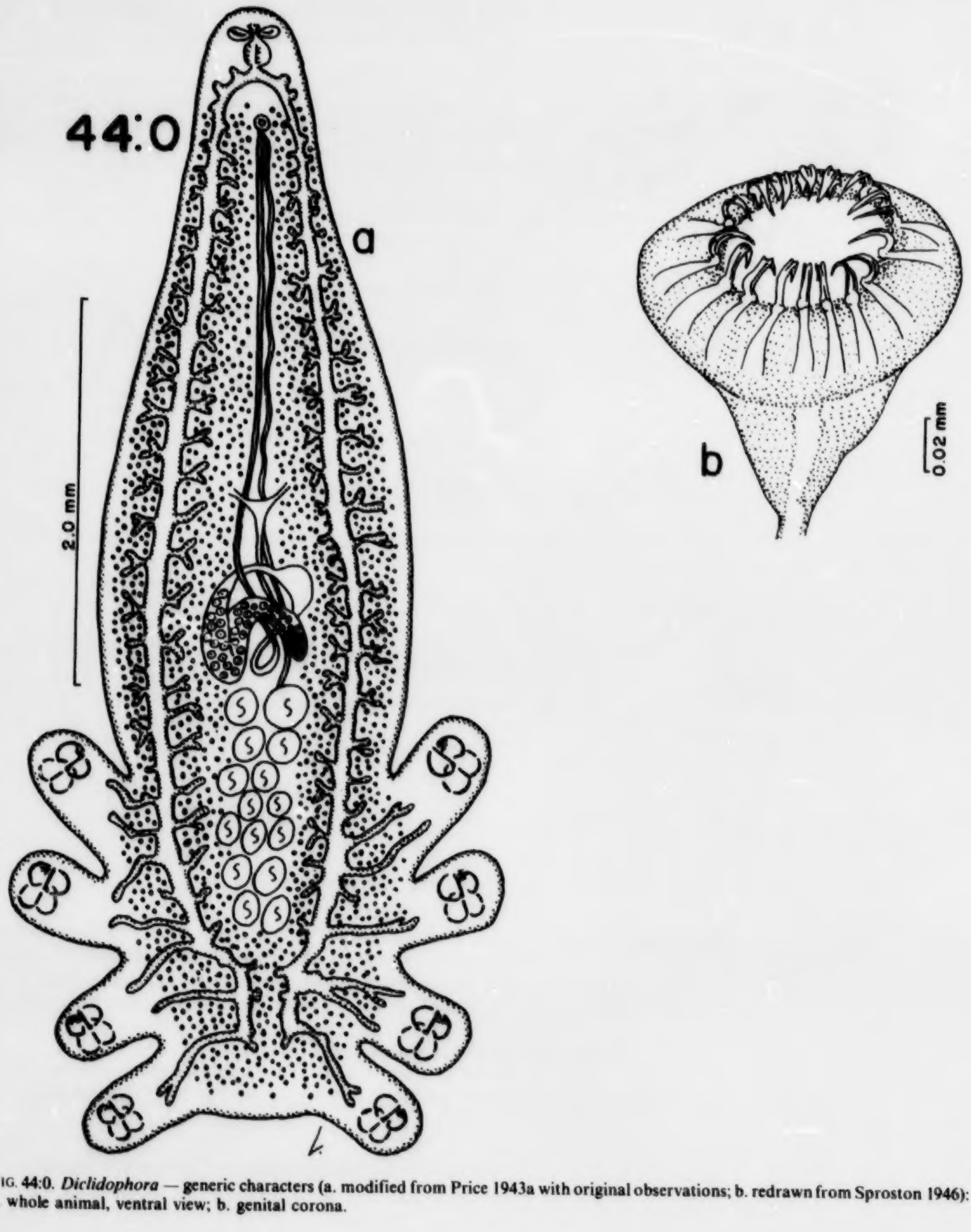
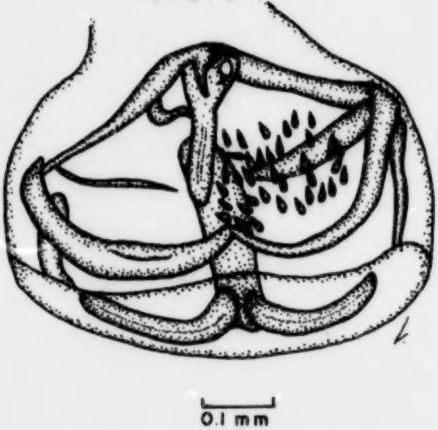
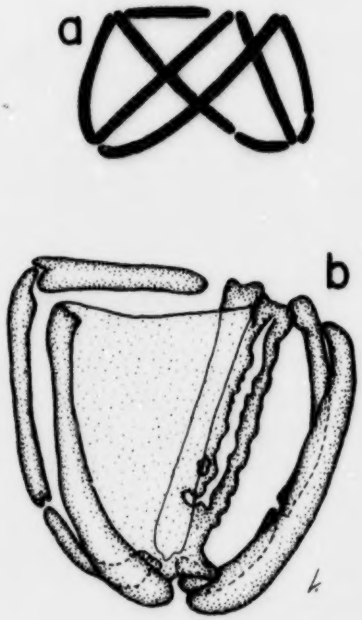


FIG. 44:0. *Diclidophora* — generic characters (a. modified from Price 1943a with original observations; b. redrawn from Sproston 1946): a. whole animal, ventral view; b. genital corona.

44:1



44:3



44:2

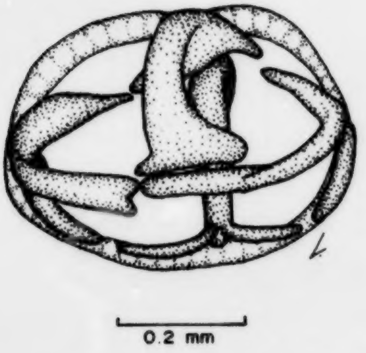


FIG. 44:1–44:3. *Diclidophora* spp. 44:1. *D. denticulata* (redrawn from Price 1943a): haptoral clamp (from left side of haptor). 44:2. *D. maccallumi* (redrawn from Price 1943a): haptoral clamp (from left side of haptor). 44:3. *D. macruri* (redrawn from Brinkmann 1942): a. schematic haptoral clamp to show position of sclerites; b. haptoral clamp.

2 **Body length more than 4 mm. Haptoral clamps dissimilar in size, increasing in diameter from anterior to posterior pair, arranged in two rows, one on either side of posterior end of body; each clamp wider than deep .... *D. maccallumi* (Price, 1943) Sproston, 1946 (Fig. 44:2)**

Descriptive and morphometric data (from Price 1943a): body 4.2–6.9 mm long by 1.5–2.1 mm maximum (midbody) width; haptor up to 1.8 mm long by 2.3 mm wide, anterior attachment organs 0.17–0.26 mm wide, posterior pair 0.43–0.51 mm wide; penis 0.04–0.10 mm diameter, corona with 13–16 spines.

On gills of *Urophycis chuss*
Records: Stafford 1904 (Atl); 1907 (Atl); Gaevskaya and Umnova 1977 (Atl)

Body length less than 4 mm. Haptoral clamps all similar in size, arranged in an arc round posterior end of body; each clamp deeper (one and a half times longer) than wide .... *D. macruri* (Brinkmann, 1942) Sproston, 1946 (Fig. 44:3)

Descriptive and morphometric data (from Brinkmann 1942): body 1.25–3.50 mm long by 0.50–0.75 mm in maximum diameter. Corona with 10–14 spines.

On [gills of] *Macrourus rupestris*
Records: Szuks 1980 (Atl); Zubchenko 1981 (Atl)

Record of unidentified *Diclidophora* sp. is listed from:

Macrourus berglax — Redkozubova 1976, Atlantic.

Macruricotyle Mamaev and Lyadov, 1975 (Fig. 45:0)

Diclidophoridae: body elongate, narrowing anteriorly, clearly separate from haptor. Haptor bilobed with four peduncles each with single clamp; terminal lappet with one or two pairs minute hooks. Adhesive callous on one or more pairs of clamps.[91] Testes numerous, postovarian; genital corona armed with spines. Ovary looping; vitellaria extending into haptoral lobes. On gills of Macrouridae. One species on Canadian fishes.

Macruricotyle newfoundlandiae Campbell, Correia and Haedrich, 1982 (Fig. 45:1)

Descriptive and morphometric data (from Campbell et al. 1982): body (excluding haptor) 3.6–8 mm by 0.36–1.00 mm maximum (ovarian level) width. Clamps 160–272 by 192–264, anterior clamps often slightly smaller. Buccal suckers 72–128 in diameter; pharynx 256–360 by 224–288. Penis 80–136 diameter; corona with 10–14 hooks.

On gills of *Macrourus berglax*
Record: Campbell et al. 1982 (Atl)

DISCOCOTYLIDAE Price, 1936

Mazocraeoidea: haptor symmetrical with four pairs of sessile, symmetrical clamps; median sclerite of clamp single, U-shaped, often conspicuous. Posterior border of haptor with one pair (I) marginal hooks. Caeca diverticulate, not confluent posteriorly. Testes usually numerous, rarely single; genital pore unarmed, genital sucker present or absent. Freshwater, on Cypriniformes and Salmoniformes.

Key to genera of Discocotylidae

1 Testis single, extensively lobed; genital sucker present. On gills of Catostomidae and Cyprinidae .... *Octomacrum*

Testes numerous, follicular; genital sucker absent 2

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[91] One pair according to Mamaev and Lyadov (1975) on *M. clavipes*; one or two pairs according to Campbell et al. (1982) for *M. newfoundlandiae*.

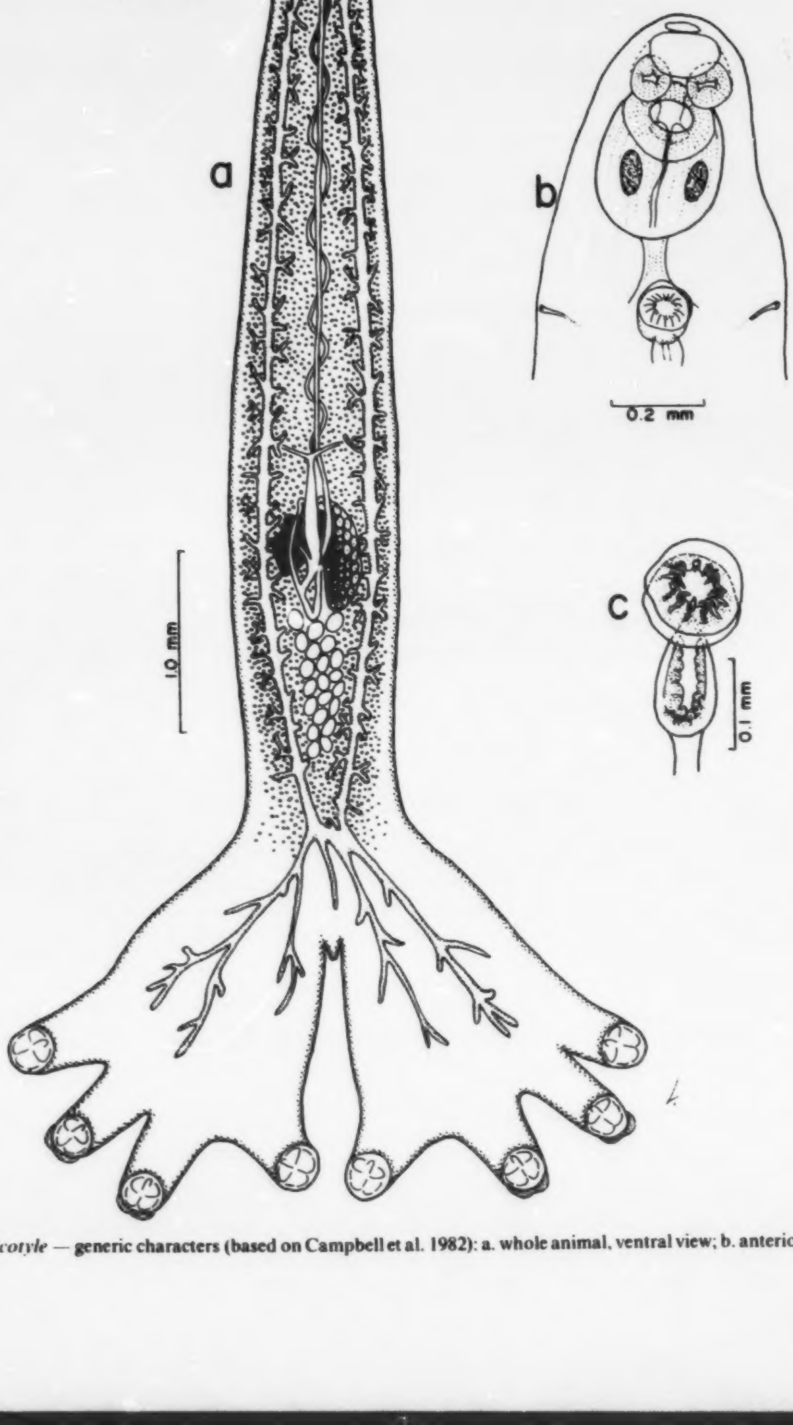
45:0
a
b
0.2 mm
1.0 mm
c
0.1 mm

FIG. 45:0. *Macruricotyle* — generic characters (based on Campbell et al. 1982): a. whole animal, ventral view; b. anterior region; c. genital corona.

45:1

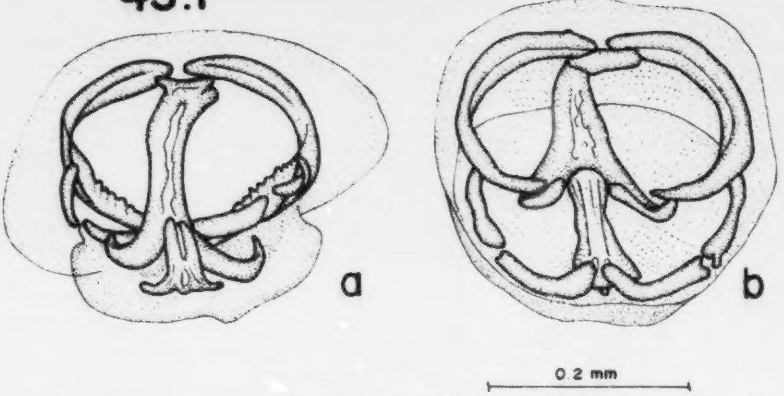

FIG. 45:1. *Macruricotyle newfoundlandiae* (redrawn from Campbell et al. 1982): a. second clamp from right side of haptor, posterior view showing callous; b. second clamp from left side of haptor, anterior view.

2 Haptor wider than long; posterior pair clamps similar in size, or only slightly smaller than anterior three pairs; vagina double, V-shaped, with two lateral openings. On gills of Salmonidae .... *Discocotyle*

Haptor not wider than long; posterior pair clamps markedly smaller (>20%) in size than anterior three pairs; vagina single with one ventral opening. On gills of Catostomidae ..... *Neodiscocotyle*

Discocotyle Diesing, 1850 (Fig. 46:0)

Discocotylidae: haptor rectangular with posterior pair of clamps equal in size (or only slightly smaller) to anterior three pairs. Testes numerous, follicular; genital sucker absent. Vagina double, V-shaped, with two lateral openings at or near level of genital pore. On gills of Salmonidae. One species on Canadian fishes.

Discocotyle sagittata (Leuckart, 1842) Diesing, 1850 (Fig. 46:1)

Descriptive and morphometric data (from Price 1943b):[92] body 5.5–7.0 mm long by 1.70 mm maximum width; buccal suckers 0.09–0.10 mm diameter; haptor 0.68–0.85 mm long by "about" 1.00 mm wide; anterior clamps 0.24–0.25 mm wide, posterior clamps 0.20–0.25 mm wide. Hamuli 0.04 mm long.

On gills of *Coregonus artedii* (2,6,16,19,20); *C. clupeaformis* (6,8,15,16,17,18,19,20); *C. hoyi* (2); *Oncorhynchus kisutch* (10,20); *Prosopium cylindraceum* (2,8,15); *P. williamsoni* (1); *Salmo gairdneri* (7); *S. salar* (3,4,8,9,11,12,13,14,17); *S. trutta* (3,5,7); *Salvelinus fontinalis* (3,5,7,8,9,17); *S. fontinalis* × *S. namaycush* (18); *S. malma* (1); *S. namaycush* (8,15); *Thymallus arcticus* (15); unspecified Salmonidae (10)

Records: 1. Bangham and Adams 1954 (BC); 2. Bangham 1955 (Ont); 3. Sandeman and Pippy 1967 (Nfld); 4. Pippy 1969 (Lab, NB-b, NB, Nfld, NS); 5. Threlfall and Hanek 1970b (Atl-?[93], Nfld-b?[94] and/or Nfld); 6. Dechtiar 1972c (Ont); 7. Hanek and Fernando 1972b (Ont); 8. Hicks and Threlfall 1973 (Lab); 9. Hare and Frantsi 1974 (NS); 10. Leong and Holmes 1974 (Alta); 11. Hare 1974 (NB); 12. Hare and Burt 1975a (NB); 13. 1975b (NB-b, NB); 14. 1976 (NB); 15. Arthur et al. 1976 (YT); 16. Watson 1977 (Man); 17. Chinniah and Threlfall 1978 (Nfld); 18. Dechtiar and Berst 1978 (Ont); 19. Lubinsky and Loch 1979 (Man); 20. Leong and Holmes 1981 (Alta)

Records of unidentified *Discocotyle* sp. are listed from:

Salmo salar, Salvelinus fontinalis — Hanek and Molnar 1974, Quebec.

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[92] As *D. salmonis* Shaffer, 1916 which was declared a synonym of *D. sagittata* by Brinkmann (1952).

[93] Threlfall and Hanek (1970b) examined *Salmo trutta* which were taken in freshwater or were sea-run. Prevalence of *D. sagittata* was tabulated as 18.1% but the source of the infected fish was not declared. Hence, the record for the Atlantic (Atl) is questionable.

[94] Threlfall and Hanek (1970b) examined *Salvelinus fontinalis* which were taken in fresh- or brackish water. Prevalence of *D. sagittata* was tabulated as 31.2% but the source of infected fish was not declared. Hence, the record for brackish water (Nfld-b) is questionable.

46:0

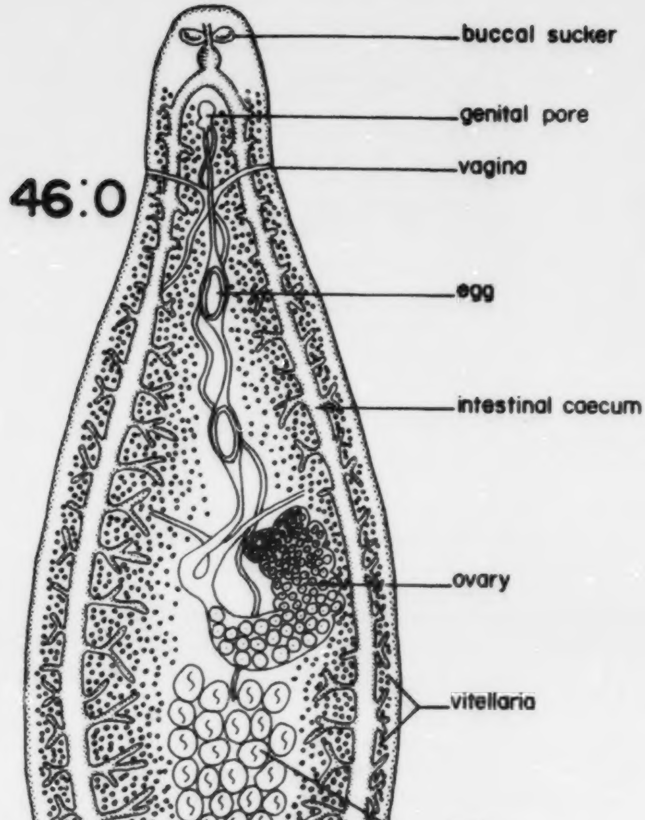
buccal sucker
genital pore
vagina
egg
intestinal caecum
ovary
vitellaria
testes
2.0 mm
haptoral clamp
marginal hook

FIG. 46:0. *Discocotyle* — generic characters (modified from Bykhovsky 1957 and Price 1943b): whole animal, ventral view.

46:1

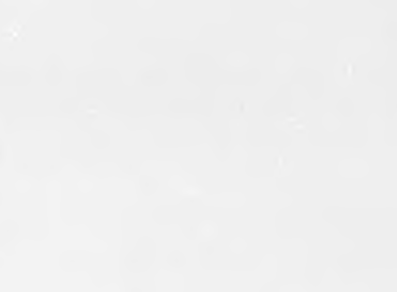

FIG. 46:1. *Discocotyle sagittata* (redrawn from Bykhovsky 1957): haptoral clamp.

Neodiscocotyle Dechtiar, 1966 (Fig. 47:0)

Discocotylidae: haptor narrowing posteriorly with posterior pair of clamps markedly smaller than anterior three pairs. Testes numerous, follicular; genital sucker absent, genital atrium with conical spines. Vagina single, opening at or on lateral margin. On gills of Catostomidae. One species on Canadian fishes.

Neodiscocotyle carpioditis Dechtiar, 1967 (Fig. 47:1)

Descriptive and morphometric data (from Dechtiar 1967): body 5.20–10.57 mm long by 1.43–1.62 mm maximum width; buccal suckers 0.16–0.26 mm diameter; haptor 1.44–1.89 mm long, "trapezoidal"; anterior clamps 0.36–0.50 mm wide, posterior clamps 0.28–0.35 mm wide. Hamuli 0.10–0.11 mm long.

On gills of *Carpiodes cyprinus*
Records: Dechtiar 1967 (Ont); 1972b (Ont)

Octomacrum Mueller, 1934 (Fig. 48:0)

Discocotylidae: haptor narrowing posteriorly with posterior pair of clamps markedly smaller than anterior three pairs. Testis single, lobulate. Genital sucker present. On gills of Cypriniformes (Catostomidae and Cyprinidae).

Key to species of *Octomacrum*

1 Haptoral clamps comparatively large (anterior pair 0.34 mm wide); distal ends of median clamp sclerite rounded or pointed .... *O. lanceatum* Mueller, 1934 (Fig. 48:1, Table 28)

On gills of *Catostomus catostomus* (5,12,13); *C. commersoni* (1,2,3,4,6,7,8,11); *C. macrocheilus* (5,9, 13,14); *Mylocheilus caurinus* (5); *Notropis cornutus* (8); *N. heterolepis* (2); *Oncorhynchus tshawytscha* (9,14); *Pimephales promelas* (10)
Records: 1. Wright 1879 (Ont?[95]); 2. Bangham 1941 (Ont); 3. 1955 (Ont); 4. Bangham and Venard 1946 (Ont); 5. Bangham and Adams 1954 (BC); 6. Dechtiar 1972b (Ont); 7. 1972c (Ont); 8. Molnar et al. 1974 (Ont); 9. Anon. 1978 (BC); 10. Black 1979 (pers. comm.) (Ont) new host record; 11. Lubinsky and Loch 1979 (Man); 12. Shepard and Mace 1980 (BC); 13. Anon. 1981 (BC); 14. Arai and Mudry 1983 (BC)

Haptoral clamps smaller (anterior pair up to 0.14 mm wide); distal ends of median clamp sclerite otherwise 2

2 Distal end of dorsal limb of median clamp sclerite heart-shaped, fenestrated. Genital sucker rectangular, 0.10–0.16 mm wide .... *O. microconfibula* Hargis, 1952 (Fig. 48:2, Table 28)

On gills of *Chrosomus eos* (4); *Mylocheilus caurinus* (2,5,6); *Notemigonus crysoleucas* (1,3,4); *Richardsonius balteatus* (5); *Semotilus margarita* (4)
Records: 1. Dechtiar 1972c (Ont); 2. Anon. 1978 (BC); 3. Lubinsky and Loch 1979 (Man); 4. Cone 1980 (NB); 5. Shepard and Mace 1980 (BC); 6. Arai and Mudry 1983 (BC)

Distal ends of dorsal and ventral limb of median clamp sclerite bifid. Genital sucker circular, 0.18–0.22 mm wide .... *O. semotili* Dechtiar 1966 (Fig. 48:3, Table 28)

On gills of *Chrosomus neogaeus* (2,3); *Semotilus atromaculatus* (1); *S. margarita* (2,3)
Records: 1. Dechtiar 1966 (Ont); 2. 1972c (Ont); 3. Lubinsky and Loch 1979 (Man)

Records of unidentified *Octomacrum* spp. are listed from:

Couesius plumbeus — Bangham and Adams (1954), British Columbia, Dechtiar (1972c), Ontario, Lubinsky and Loch (1979), Manitoba; *Hybognathus hankinsoni* — Bangham (1941), Ontario; *Richardsonius balteatus* — Bangham and Adams (1954), British Columbia; *Semotilus atromaculatus*,[96] *S. margarita* — Bangham and Venard (1946), Ontario.

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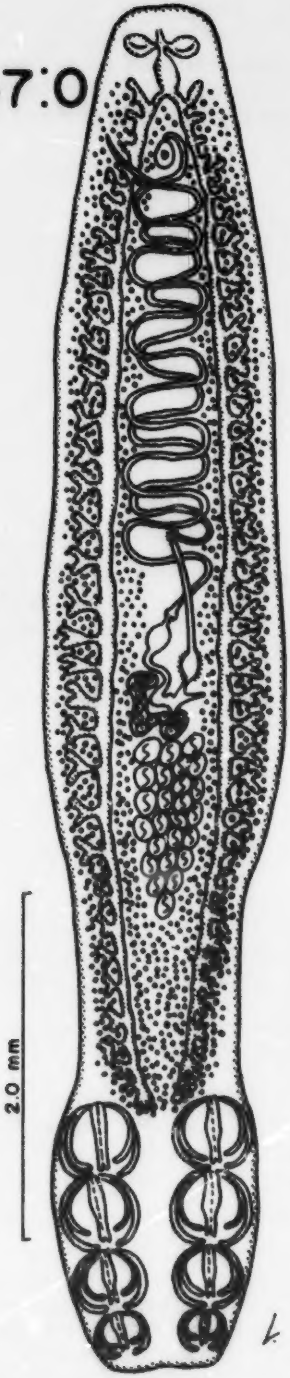
[95] As *Octobothrium sagittatum* from hosts tentatively identified as *C. commersoni* from an unknown locality.

[96] Dechtiar (1966) speculated that this record of *Octomacrum* sp. from *S. atromaculatus* may have been referable to *O. semotili*.

47:0



47:1

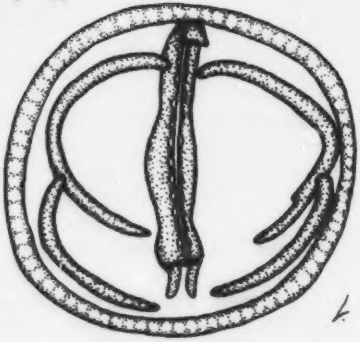


FIG. 47:0. *Neodiscocotyle* — generic characters (modified from Dechtiar 1967): whole animal, ventral view.

FIG. 47:1. *Neodiscocotyle carpioditis* (redrawn from Dechtiar 1967): haptoral clamp.

48:0

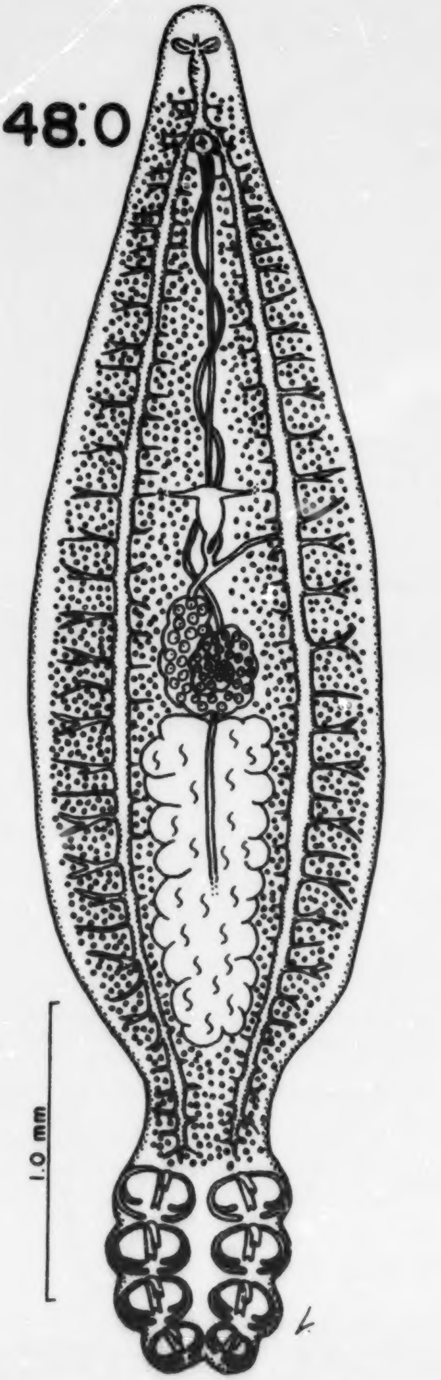


Fig. 48:0. *Octomacrum* — generic characters (modified from Price 1943b with original observations): whole animal, ventral view.

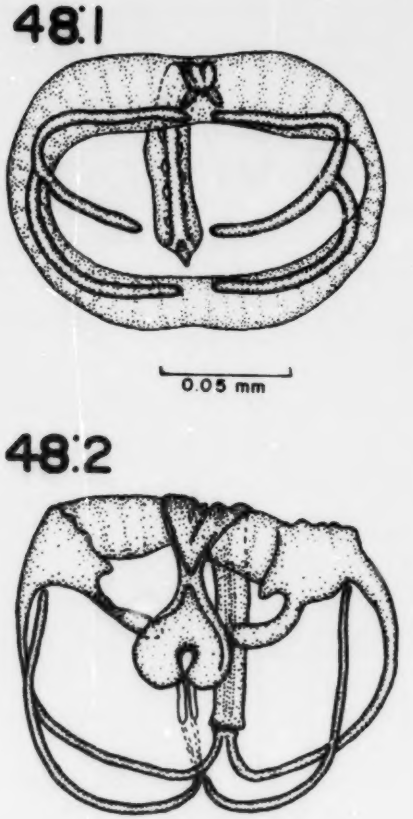


Fig. 48:1–48:3. *Octomacrum* spp. 48:1. *O. lanceatum* (redrawn from Mueller 1934): haptoral clamp. 48:2. *O. microconfibula* (redrawn from Hargis 1952): haptoral clamp. 48:3. *O. semotili* (redrawn from Dechtiar 1966): haptoral clamp.

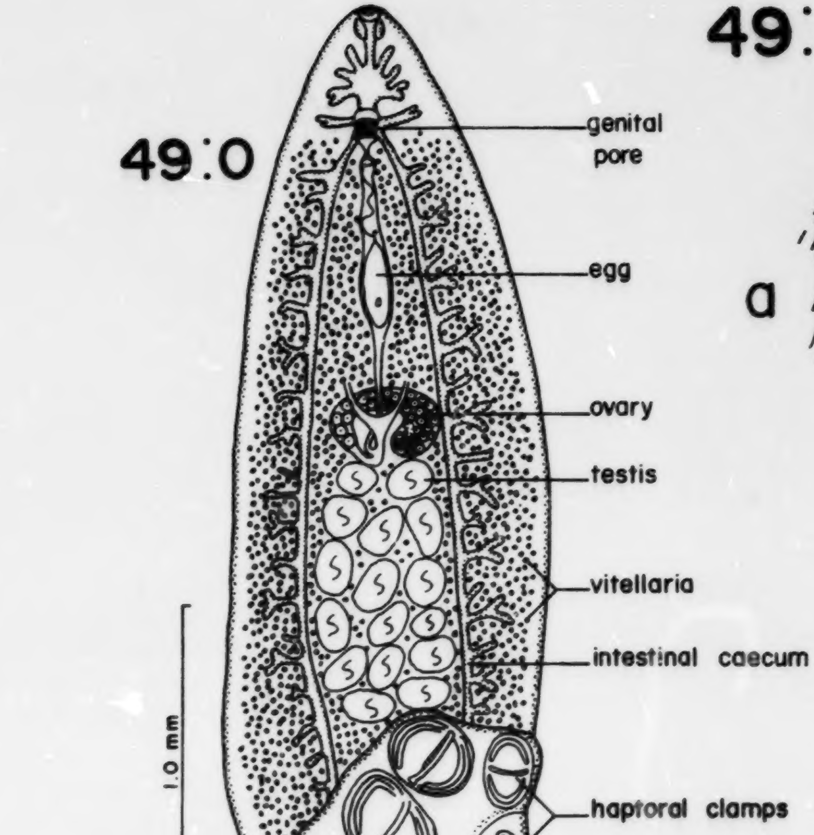

49:0
genital pore
egg
ovary
testis
vitellaria
intestinal caecum
haptoral clamps
1.0 mm

FIG. 49:0. *Lintaxine* — generic characters (modified from Price 1962 with original observations): whole animal, ventral view.

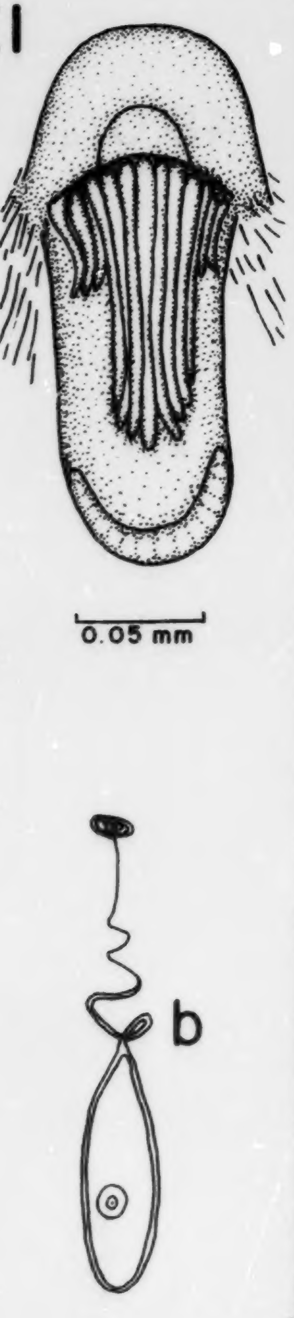

49:1
a
0.05 mm
b
0.2 mm

FIG. 49:1. *Lintaxine cokeri* (redrawn from Price 1962): a. genital spines; b. egg.

TABLE 28. Comparative measurements (in mm) of the species of *Octomacrum* Mueller, 1934, recorded from fishes of Canada.

Species	*Octomacrum lanceatum*	*Octomacrum microconfibula*	*Octomacrum semotili*
Source of data	Mueller (1934)	Hargis (1952)	Dechtiar (1966)
Body: length	5.0–6.0	4.35 (2.50–6.00)	3.19 (2.50–3.60)
width	1.5–2.0	0.91 (0.52–1.40)	0.94 (0.59–1.41)
Buccal suckers: width	0.10	0.05 (0.04–0.06)	0.06 (0.06–0.08)
Haptor: length	0.80	0.37 (0.31–0.39)	0.33 (0.27–0.38)
width	0.69	0.60 (0.30–0.92)	0.37 (0.33–0.43)
Clamps — anterior pair: width	0.34	0.11 (0.09–0.12)	0.12 (0.11–0.14)
posterior pair: width	— (smaller than anterior pair)	0.08 (0.05–0.10)	0.10 (0.09–0.11)
Site	gills	gills	gills
Hosts	*Catostomus catostomus* *C. commersoni* *C. macrocheilus* *Mylocheilus caurinus* *Notropis cornutus* *N. heterolepis* *Oncorhynchus tshawytscha* *Pimephales promelas*	*Chrosomus eos* *Mylocheilus caurinus* *Notemigonus crysoleucas* *Richardsonius balteatus* *Semotilus margarita*	*Chrosomus neogaeus* *Semotilus atromaculatus* *S. margarita*
Locality(ies)	British Columbia Manitoba Ontario	British Columbia Manitoba New Brunswick Ontario	Manitoba Ontario

HETERAXINIDAE Price, 1962[97]

Mazocraeoidea: haptor well developed, asymmetrical, usually triangular, each lateral margin with single row of clamps; longer/larger side usually carries more clamps; median clamp sclerite single, U-shaped, often bifid or trifid distally. Caeca diverticulate. Testes numerous, follicular; postovarian. Ovary U-shaped with extremities not oriented anteriorly. Freshwater, on Perciformes. One genus, *Lintaxine*, on Canadian fishes.

Lintaxine Sproston, 1946 (Fig. 49:0)

Heteraxinidae: sides of haptor not greatly different in length; clamps of one lateral margin fewer but larger. Genital pore armed. Vitellaria extending into haptor. On gills of Sciaenidae. One species on Canadian fishes.

Lintaxine cokeri (Linton, 1940) Sproston, 1946 (Fig. 49:1)

Descriptive and morphometric data (from Price 1962): body 5 mm long by 1 mm wide; haptor 2.7 mm long with 10–11 clamps, 0.21–0.50 mm wide, on right side and 31–33 clamps, 0.13–0.14 mm wide, on left.

On gills of *Aplodinotus grunniens*
Record: Dechtiar 1972b (Ont)

MAZOCRAEIDAE Price, 1936

Mazocraeoidea: clamps either on discrete, symmetrical haptor or on lateral margins of body; median clamp sclerite in three distinct parts forming "fair-lead" system.[98] Posterior border of haptor, forming a small lappet or not, with one pair of hamuli and one or two pairs (I and II) marginal hooks. Caeca diverticulate, not confluent posteriorly, extending to posterior margin of body or not. Testes several, follicular, or single; genital pore armed. Marine or freshwater, on Clupeiformes, Osteoglossiformes, and Perciformes.

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[97] Kritsky et al. (1978b) discussed the systematic status of the family Heteraxinidae.

[98] See Llewellyn (1957).

Keys to genera of Mazocraeidae

1 Testes several; clamps situated along lateral margins of haptor which is clearly separated from body .... *Kuhnia*

Testis single; clamps situated along lateral margins of posterior body region 2

2 Body broad; testis opposite ovary; clamps extending anteriorly beyond level of ovary .... *Mazocraeoides*

Body not markedly broad; testis posterior to ovary; clamps not extending anteriorly to level of ovary .... *Pseudomazocraeoides*

Kuhnia Sproston, 1945 (Fig. 50:0, 50:1)

Mazocraeidae: body lanceolate; clamps situated on lateral margins of haptor, posterior border of haptor with one pair of hamuli and two pairs (I and II) marginal hooks. Caeca diverticulate, not extending into posterior half of haptor. Testes several, postovarian; genital bulb with two longitudinal rows of inwardly curving hooks and pair anterolateral protuberances each bearing curved hook with two alate spines. Ovary looping; vitellaria follicular, not extending into haptor. On gills of Scombridae. One species on Canadian fishes.

Kuhnia scombri (Kuhn, 1829) Sproston, 1945 (Fig. 50:2)

Descriptive and morphometric data (from Sproston 1945): body 1.3–6.5 mm long, width 10–17% of length; haptor 0.23–0.62 mm long (about 9% of body length in adults); clamps 42–52 diameter, hamuli 112–120 long.

On gills of *Scomber scombrus*
Records: Stafford 1904 (Atl); 1907 (Atl)

Mazocraeoides Price, 1936 (Fig. 51:0)

Mazocraeidae: body broad; clamps on lateral body margins with anterior pair anterior to level of ovary; terminal lappet with one pair of hamuli and two pairs (I and II) marginal hooks. Caeca diverticulate, extending almost to posterior body margin. Testis single, lateral to ovary; genital pore with two longitudinal rows of inwardly curving hooks and one pair of lateral spines. Ovary looping, vitellaria extending almost to posterior body margin. On gills of Clupeidae and Hiodontidae. One species on Canadian fishes.

Mazocraeoides olentangiensis Sroufe, 1959 (Fig. 51:1)

Descriptive and morphometric data (from Sroufe 1958): body 1.2 (1.0–1.8) mm long by 0.4 (0.3–0.6) mm maximum width; clamps 48 (40–61) long by 58 (49–75) wide; hamuli 63 (58–67) long; marginal hooks, pair I 27 (22–27) long, pair II 8 (7–10) long. Genital corona 22 (20–29) wide, inner hooks of corona in two rows of five each; outer hooks of corona 15 (14–16) long.

On gills of *Dorosoma cepedianum*
Record: Dechtiar 1972b (Ont)

Record of an unidentified *Mazocraeoides* sp. is listed from:

Hiodon tergisus — Dechtiar 1972b, Ontario.

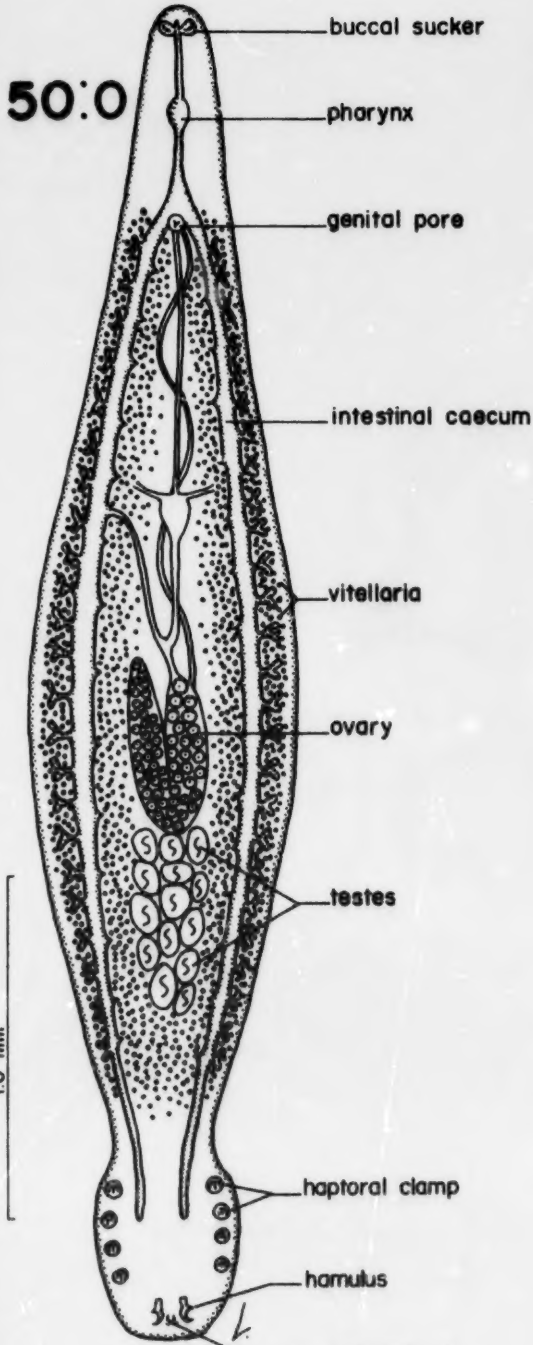

50:0
buccal sucker
pharynx
genital pore
intestinal caecum
vitellaria
ovary
testes
1.0 mm
haptoral clamp
hamulus
marginal hook

FIG. 50:0. *Kuhnia* — generic characters (modified from Sproston 1945): whole animal, ventral view.

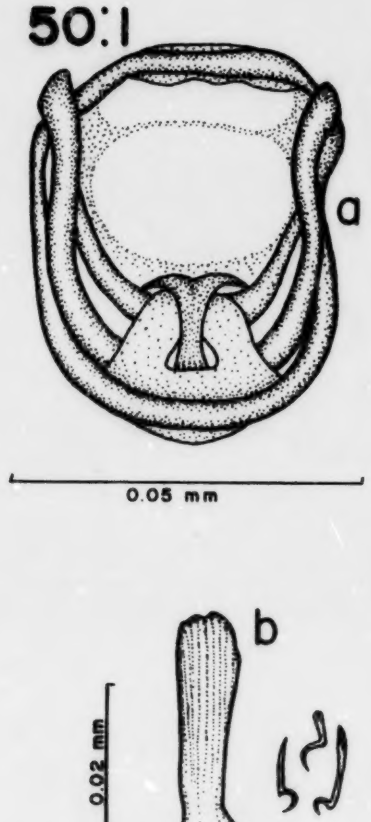

50:1
a
0.05 mm
b
0.02 mm
c
0.02 mm

FIG. 50:1. *Kuhnia scombri* (redrawn from Sproston 1946): a. haptoral clamp; b. hamulus and marginal hooks; c. genital spines.

50:2

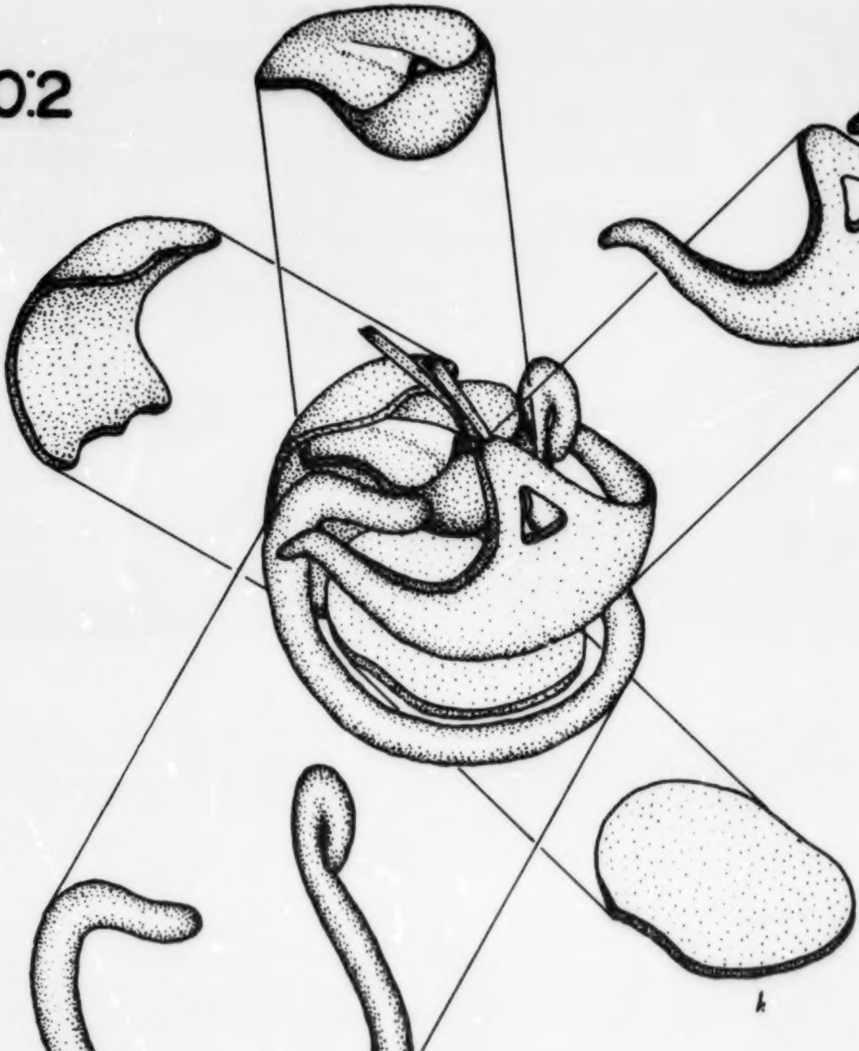


FIG. 50:2. *Kuhnia* — haptoral clamp (three-dimensional reconstruction after Llewellyn 1957).

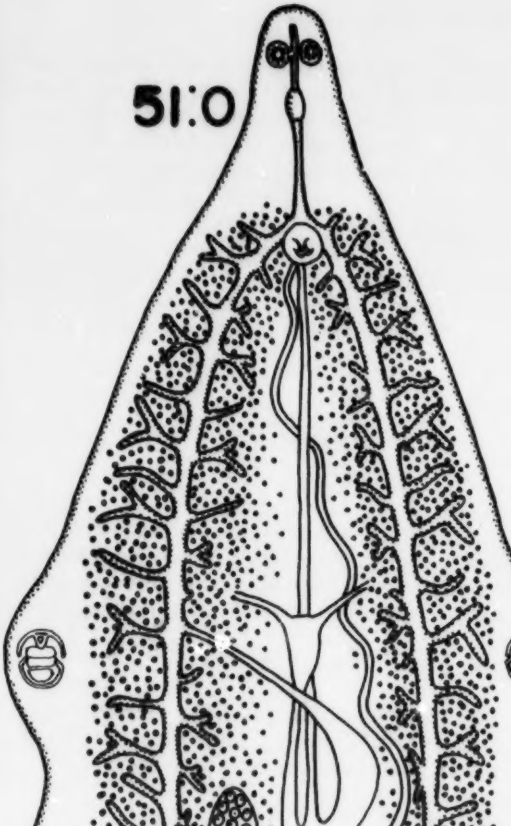


FIG. 51:0. *Mazocraeoides* — generic characters (modified from Sroufe 1958 with original observations): whole animal, ventral view.

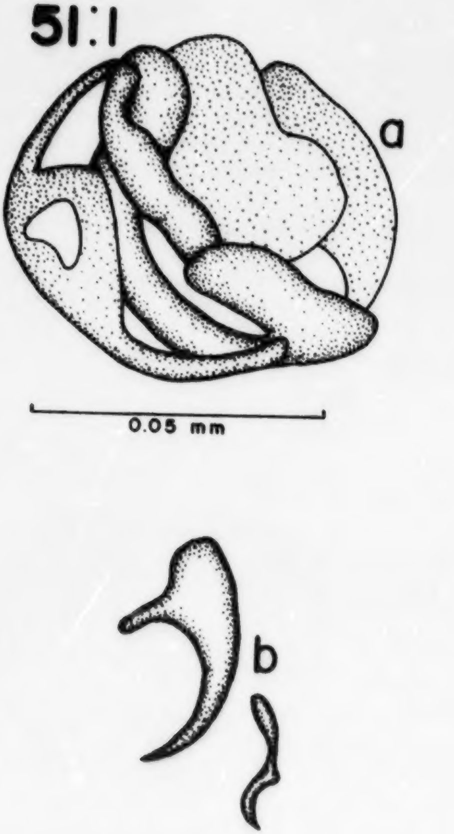

51:1
a
0.05 mm
b
0.05 mm
c
0.03 mm

FIG. 51:1. *Mazocraeoides olentangiensis* (redrawn from Sroufe 1958): a. haptoral clamp; b. hamulus and marginal hook; c. genital spines.

Pseudomazocraeoides Price, 1961 (Fig. 52:0)

Mazocraeidae: body not markedly broad; clamps situated along lateral body margins, with anterior pair posterior to level of ovary; terminal lappet with one pair hamuli and one pair (I) marginal hooks. Caeca diverticulate, extending almost to posterior margin of body. Testis single, lobed, postovarian; genital pore with two longitudinal rows of inwardly curving hooks and one pair of lateral spines. Ovary looping, vitellaria extending almost to posterior body margin. On gills of Clupeidae. One species on Canadian fishes.

Pseudomazocraeoides ontariensis Hanek and Fernando, 1971 (Fig. 52:1)

Descriptive and morphometric data (from Hanek and Fernando 1971a, holotype and, in parentheses, range): body 2.4 (1.8–2.4) mm long by 0.72 (0.72) mm maximum width; clamps 59 (59–62) long by 74 (73–82) wide; hamuli 63 (63–65) long; marginal hooks, pair I 23 (23–26) long. Genital corona 24 (24–26) wide, inner hooks of corona in two rows of five each; outer hooks of corona 8 (8–9) long.

On gills of *Dorosoma cepedianum*
Record: Hanek and Fernando 1971a (Ont)

MICROCOTYLIDAE Taschenberg, 1897

Mazocraeoidea: haptor symmetrical, each lateral margin with single row of numerous clamps; median sclerite of clamp single, U-shaped, often bifid distally. Caeca diverticulate, confluent posteriorly, with median branch extending into haptor. Testes numerous, follicular, postovarian. Ovary U-shaped with extremities oriented posteriorly. Marine and freshwater, on Perciformes. One genus, *Microcotyle*, on Canadian fishes.

Microcotyle van Beneden and Hesse, 1863 (Fig. 53:0, 53:1)

Microcotylidae: lateral margins of haptor not frilled and not extending anteriorly into body region; hamuli and marginal hooks absent. Vitellaria entirely or largely coextensive with gut caeca. Marine or (more rarely) freshwater, on gills of Perciformes (Hexagrammidae, Sciaenidae, Scorpaenidae, Stromateidae).

Key to species of *Microcotyle*

1 Anterior haptoral clamps situated behind midbody level (Fig. 53:1a, 1b). On marine fishes 2

Anterior haptoral clamps situated at midbody level (Fig. 53:1c). On freshwater fish (*Aplodinotus grunniens*: Sciaenidae) 3

2 Haptor with 23–31 clamps in each row; each clamp 0.09–0.12 mm diameter .... *M. sebastis* Goto, 1894 (Fig. 53:3, Table 29)

On gills of *Hexagrammos lagocephalus* (1,2); *Sebastes alutus* (3,4); *S. brevispinis* (4); *S. caurinus* (2,4); *S. diploproa* (4); *S. elongatus* (2,4); *S. helvomaculatus* (4); *S. maliger* (4); *S. nigrocinctus* (4); *S. paucispinis* (4); *S. proriger* (4); *S. reedi* (4); *S. variegatus* (4); *S. wilsoni* (4); *S. zacentrus* (4)
Records: 1. Arai 1967 (Pac); 2. 1969 (Pac); 3. Sekerak and Arai 1973 (Pac); 4. 1977 (Pac)

Haptor with 60 clamps in each row; each clamp 0.05 mm diameter. On *Peprilus triacanthus* .... *M. poronoti* MacCallum, 1915 (Fig. 53:2, Table 29)

On gills of *Peprilus triacanthus*
Record: Cooper 1915 (Atl)

52:0

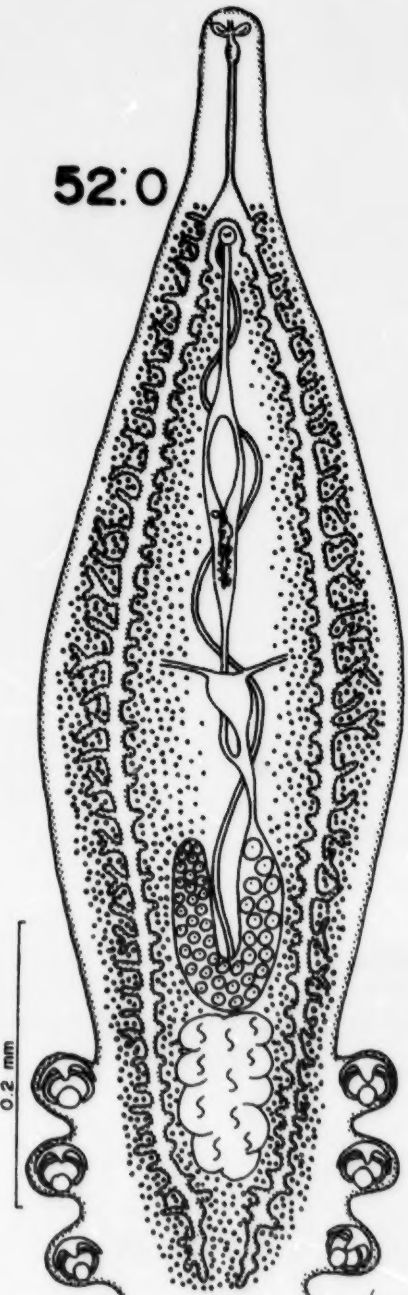


FIG. 52:0. *Pseudomazocraeoides* -- generic characters (modified from Hanek and Fernando 1971a): whole animal, ventral view.

52:1

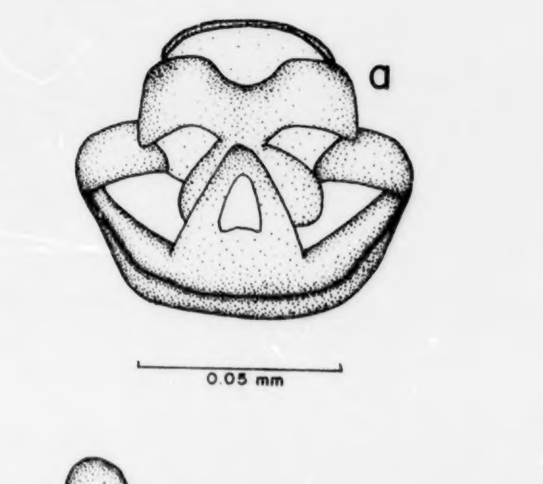
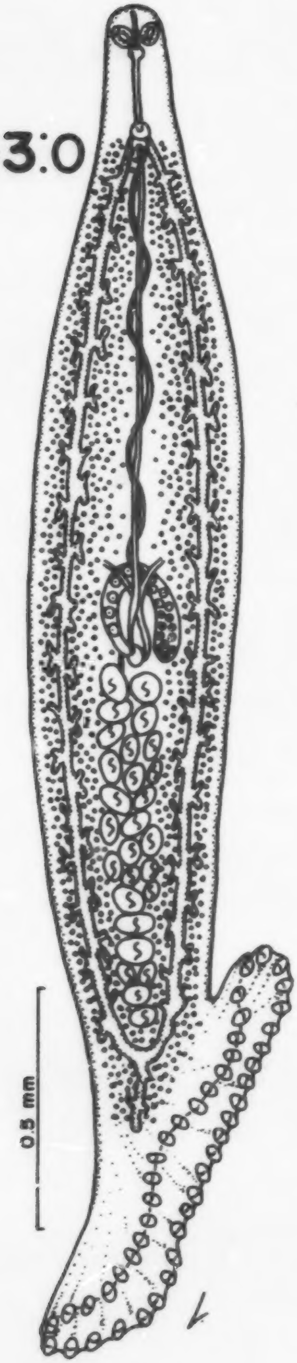


FIG. 52:1. *Pseudomazocraeoides ontariensis* (redrawn from Hanek and Fernando 1971a): a. haptoral clamp; b. hamulus and marginal hook; c. genital spines.

53:0



53:1

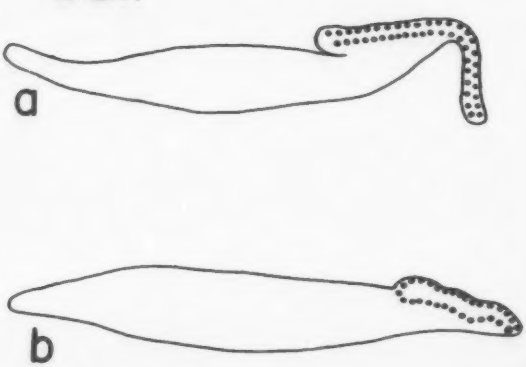
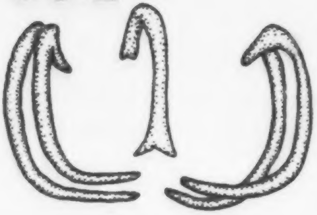


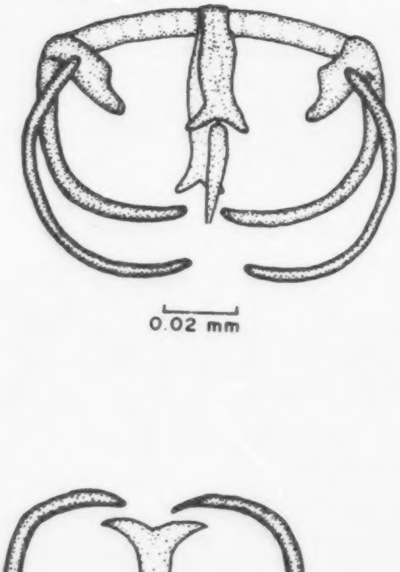
FIG. 53:0. *Microcotyle* — generic characters (modified from MacCallum 1915): whole animal, ventral view.

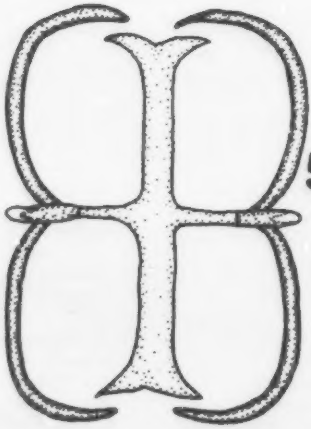
FIG. 53:1. Schematic comparison of *Microcotyle* spp. (original): a. *M. poronoti*; b. *M. sebastis*; c. *M. spinicirrus*/*M. eriensis*.

53:2



53:3





53:4

FIG. 53:2–53:4. *Microcotyle* spp. 53:2. *M. poronoti* (redrawn from MacCallum 1915): haptoral clamp. 53:3. *M. sebastis* (redrawn from Bonham and Guberlet 1937): haptoral clamp. 53:4. *M. spinicirrus* (redrawn from Bangham and Hunter 1936): haptoral clamp.

3 **Haptor with 21–23 clamps in each row. Testes 15–20 in number** .... ***M. eriensis*** **Bangham and Hunter, 1936 (Table 29)**

On gills of *Aplodinotus grunniens*
Record: Bangham and Hunter 1939 (Ont)

Haptor with 40–45 clamps in each row. Testes 35–45 in number .... ***M. spinicirrus*** **MacCallum, 1918 (Fig. 53:4, Table 29)**

On [gills of] *Aplodinotus grunniens*
Record: Bangham and Hunter 1939 (Ont)

Records of unidentified *Microcotyle* spp. are listed from:

Sebastes alutus — Sekerak and Arai 1977, Pacific; *S. caurinus* — Hoskins et al. 1976, Pacific.

Records of unidentified Monogenea gen. spp. are listed from:

Oncorhynchus kisutch, unspecified skate — Hoskins and Hulstein 1977, Pacific; *Catostomus catostomus* — Anon. 1981, British Columbia.

TABLE 29. Comparative measurements (in mm) of *Microcotyle* spp. (Microcotylidae) recorded from fishes of Canada.

Species	*M. eriensis*	*M. poronoti*	*M. sebastis*	*M. spinicirrus*
Source of data	Bangham and Hunter (1936)	MacCallum (1915)	Bonham and Guberlet (1937)	Bangham and Hunter (1936)
Body: length	1.2–2.7	6	3.9 (3.1–4.6)	2.3–2.5
width	0.4–0.65	0.80	0.86 (0.64–1.05)	0.5–0.7
Haptor: length	—	2.50	1.3 (0.95–1.70)	—
Clamps right side:				
number	21–23[a]	60	30 (23–31)	40–45[b]
size	—	0.05	0.10 (0.09–0.12)	—
Clamps left side:				
number	21–23[a]	60	30 (23–31)	40–45[b]
size	—	0.05	0.10 (0.09–0.12)	—
Testes: number	15–20	32	32 (21–48)	35–45
Site	gills	gills	gills	gills
Host(s)	*Aplodinotus grunniens*	*Peprilus triacanthus*	*Hexagrammos lagocephalus* *Sebastes alutus* *S. brevispinis* *S. caurinus* *S. diploproa* *S. elongatus* *S. helvomaculatus* *S. maliger* *S. nigrocinctus* *S. paucispinus* *S. proriger* *S. reedi* *S. variegatus* *S. wilsoni* *S. zacentrus*	*Aplodinotus grunniens*
Locality	Ontario	Atlantic	Pacific	Ontario

[a] Total number of clamps quoted as 42–46.
[b] Total number of clamps quoted as 80–90.

HOST-MONOGENEAN PARASITE LIST[99]

CLASS CHONDRICHTHYES

ORDER SQUALIFORMES

Family SQUALIDAE

Squalus acanthias Linnaeus   spiny dogfish
Microbothrium apiculatum (Atl)
Squalonchocotyle abbreviata (Atl)

ORDER RAJIFORMES

Family RAJIDAE

Raja laevis Mitchill   barndoor skate
Micropharynx parasitica (Atl)†

Raja radiata Donovan   thorny skate
Micropharynx parasitica (Atl)†
Pseudacanthocotyla verrilli (Atl)
Rajonchocotyloides emarginata (Atl)

Rajidae of Undetermined Species

"Skate"
Monogenea gen. sp. (BC aquarium)

CLASS OSTEICHTHYES

ORDER ACIPENSERIFORMES

Family ACIPENSERIDAE

Acipenser brevirostrum Lesueur   shortnose sturgeon
Diclybothrium armatum (NB)

Acipenser fulvescens Rafinesque   lake sturgeon
Diclybothrium armatum (Man, Ont)
D. hammulatum (Ont)
Paradiclybothrium sp. (Ont)*

Acipenser oxyrhynchus Mitchill   Atlantic sturgeon
Nitzschia sturionis (NB)

ORDER CLUPEIFORMES

Family CLUPEIDAE

Clupea harengus pallasi Valenciennes   Pacific herring
Gyrodactyloidea gen. sp. (Pac)
Gyrodactyloides petruschewskii (Pac)
Gyrodactylus harengi (Pac)

Dorosoma cepedianum (Lesueur)   gizzard shad
Mazocraeoides olentangiensis (Ont)
Pseudomazocraeoides ontariensis (Ont)

ORDER OSTEOGLOSSIFORMES

Family HIODONTIDAE

Hiodon tergisus Lesueur   mooneye
Mazocraeoides sp. (Ont)

ORDER SALMONIFORMES

Family SALMONIDAE

Coregonus artedii Lesueur   cisco or lake herring
Discocotyle sagittata (Alta, Man, Ont)

Coregonus clupeaformis (Mitchill)   lake whitefish
Discocotyle sagittata (Alta, Lab, Man, Nfld, Ont, YT)

Coregonus hoyi (Gill)   bloater
Discocotyle sagittata (Ont)

Oncorhynchus gorbuscha (Walbaum)   pink salmon
Laminiscus strelkowi (Pac, BC-b)

Oncorhynchus kisutch (Walbaum)   coho salmon
Discocotyle sagittata (Alta)
Gyrodactyloidea gen. sp. (Pac, BC)
Gyrodactylus salmonis (BC)
Monogenea gen. sp. (Pac)
Tetraonchus alaskensis (BC)

Oncorhynchus nerka (Walbaum)   sockeye salmon
Gyrodactylus nerkae (BC)
Gyrodactylus sp. (BC)
Laminiscus strelkowi (Pac, BC-b)

Oncorhynchus tshawytscha (Walbaum)   chinook salmon
Octomacrum lanceatum (BC)

Prosopium coulteri (Eigenmann and Eigenmann)   pygmy whitefish
Tetraonchus variabilis (BC)

Prosopium cylindraceum (Pallas)   round whitefish
Discocotyle sagittata (Lab, Ont, YT)
Tetraonchus variabilis (Lab, Ont, YT)

Prosopium williamsoni (Girard)   mountain whitefish
Discocotyle sagittata (BC)
Gyrodactyloidea gen. sp. (BC)
Tetraonchus variabilis (BC)

Salmo clarki Richardson   cutthroat trout
Gyrodactyloidea gen. sp. (BC)
Gyrodactylus sp. (BC)
Gyrodactylus salmonis (BC)

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[99] Parasitic Turbellaria are also listed: designated thus†.

- *Salmo gairdneri* Richardson rainbow trout
  - *Discocotyle sagittata* (Ont)
  - *Gyrodactylus avalonia* (NS)
  - *G. colemanensis* (Nfld)
  - *G. salmonis* (NS)
  - *Gyrodactylus* sp. (BC, NS)

- *Salmo salar* Linnaeus Atlantic salmon
  - *Discocotyle sagittata* (Lab, NB-b, NB, Nfld, NS)
  - *Discocotyle* sp. (Que)
  - *Gyrodactylus salmonis* (NS)
  - *Gyrodactylus* sp. (NB, NS)

- *Salmo trutta* Linnaeus brown trout
  - *Discocotyle sagittata* (Atl-?[100], Nfld, Ont)

- *Salvelinus alpinus* (Linnaeus) Arctic char
  - *Tetraonchus alaskensis* (NWT, YT)

- *Salvelinus fontinalis* (Mitchill) brook trout
  - *Discocotyle sagittata* (Lab, Nfld-b?[101], Nfld, NS, Ont)
  - *Discocotyle* sp. (Que)
  - *Gyrodactylus avalonia* (Nfld-b)
  - *G. colemanensis* (NS)
  - *G. salmonis* (NS)
  - *Gyrodactylus* sp. (Lab, NS)
  - *Tetraonchus variabilis* (Lab)

- *Salvelinus fontinalis* × *S. namaycush* splake
  - *Discocotyle sagittata* (Ont)

- *Salvelinus malma* (Walbaum) Dolly Varden
  - *Discocotyle sagittata* (BC)
  - Gyrodactyloidea gen. sp. (BC)
  - *Tetraonchus alaskensis* (BC, YT)

- *Salvelinus namaycush* (Walbaum) lake trout
  - *Discocotyle sagittata* (Lab, YT)
  - *Tetraonchus monenteron* (Lab)

- *Thymallus arcticus* (Pallas) Arctic grayling
  - *Discocotyle sagittata* (YT)
  - Gyrodactyloidea gen. sp. (BC)
  - *Tetraonchus borealis* (BC, Sask, YT)

Salmonidae of Undetermined Species

- Salmonidae gen. sp.
  - *Discocotyle sagittata* (Alta)
  - *Tetraonchus variabilis* (Ont)

Family OSMERIDAE

- *Mallotus villosus* (Müller) capelin
  - *Gyrodactyloides andriaschewi* (Atl)
  - *G. petruschewskii* (Atl)
  - *Laminiscus gussevi* (Atl)

Family UMBRIDAE

- *Umbra limi* (Kirtland) central mudminnow
  - *Gyrodactylus limi* (Ont)

Family ESOCIDAE

- *Esox lucius* Linnaeus northern pike
  - Gyrodactyloidea gen. sp. (Ont)
  - *Tetraonchus monenteron* (Alta, Lab, Man, Ont, YT)

- *Esox masquinongy* Mitchill muskellunge
  - Gyrodactyloidea gen. sp. (Ont)
  - *Tetraonchus loftusi* (Ont)

ORDER CYPRINIFORMES

Family CYPRINIDAE

- *Acrocheilus alutaceus* Agassiz and Pickering chiselmouth
  - *Dactylogyrus vancleavei* (BC)
  - Gyrodactyloidea gen. sp. (BC)

- *Carassius auratus* (Linnaeus) goldfish
  - *Dactylogyrus anchoratus* (Ont)
  - *D. vastator* (Ont)

- *Chrosomus eos* Cope northern redbelly dace
  - *Cleidodiscus brachus* (NB)
  - *Dactylogyrus chrosomi* (Ont)
  - *D. eos* (Ont, NB)
  - Gyrodactyloidea gen. sp. (Ont)
  - *Gyrodactylus* sp. (NB)
  - *Octomacrum microconfibula* (NB)

- *Chrosomus neogaeus* (Cope) finescale dace
  - *Cleidodiscus brachus* (Man, Ont)
  - Gyrodactylidae gen. sp. (Ont)
  - *Octomacrum semotili* (Man, Ont)

- *Couesius plumbeus* (Agassiz) lake chub
  - *Cleidodiscus brachus* (Lab)
  - *Dactylogyrus banghami* (BC, Ont)
  - *D. mylocheilus* (BC, Man, Ont)
  - Gyrodactyloidea gen. sp. (BC)
  - *Gyrodactylus aldrichi* (Lab)
  - *G. couesius* (BC)
  - *G. plumbeae* (Lab)
  - *Octomacrum* sp. (BC, Man, Ont)

- *Cyprinus carpio* Linnaeus common carp
  - *Dactylogyrus anchoratus* (BC, Ont)
  - *D. extensus* (BC, NS, Ont)
  - Gyrodactyloidea gen. sp. (BC)
  - *Pseudacolpenteron pavlovskii* (Ont)

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[100] See footnote 92.

[101] See footnote 93.

Hybognathus hankinsoni Hubbs	brassy minnow
Dactylogyrus hankinsoni (Ont)	
Dactylogyrus sp. (Ont)	
Gyrodactylus sp. (Ont)	
Octomacrum sp. (Ont)*	
Mylocheilus caurinus (Richardson)	peamouth
Dactylogyrus mylocheilus (BC)	
Gyrodactyloidea gen. sp. (BC)	
Octomacrum lanceatum (BC)	
O. microconfibula (BC)	
Nocomis biguttatus (Kirtland)	hornyhead chub
Dactylogyrus sp. (Ont)	
Gyrodactylus sp. (Ont)	
Nocomis micropogon (Cope)	river chub
Dactylogyrus aviunguis (Ont)	
D. flagristylus (Ont)	
D. lachneri (Ont)	
D. reciprocus (Ont)	
Notemigonus crysoleucas (Mitchill)	golden shiner
Dactylogyrus aureus (Ont)	
D. bulbus (NB)	
D. parvicirrus (Man, NB, Ont)	
Gyrodactyloidea gen. sp. (Ont)	
Octomacrum microconfibula (Man, NB, Ont)	
Notropis anogenus Forbes	pugnose shiner
Gyrodactylus sp. (Man, Ont)	
Notropis atherinoides Rafinesque	emerald shiner
Dactylogyrus sp. (Ont)	
Gyrodactyloidea gen. sp. (Ont)	
Notropis cornutus (Mitchill)	common shiner
Dactylogyrus banghami (BC, Ont)	
D. bulbus (NB, Ont)	
D. bullosus (Ont)	
D. cornutus (Ont)	
D. dubius (Ont)	
D. luxili (Ont)	
D. perlus (Ont)	
D. pollex (Ont)	
Dactylogyrus sp. (Ont)	
Gyrodactylidae gen. sp. (Ont)	
Gyrodactyloidea gen. sp. (Ont)	
Gyrodactylus sp. (Ont)	
Octomacrum lanceatum (Ont)	
Notropis heterolepis Eigenmann and Eigenmann	blacknose shiner
Dactylogyrus heterolepis (Ont)	
Dactylogyrus sp. (NB, Ont)	
Gyrodactylidae gen. sp. (Ont)	
Gyrodactyloidea gen. sp. (Ont)	
Octomacrum lanceatum (Ont)	
Notropis hudsonius (Clinton)	spottail shiner
Dactylogyrus sp. (Man, Ont)	
Gyrodactyloidea gen. sp. (Ont)	
Gyrodactylus sp. (Ont)	
Notropis rubellus (Agassiz)	rosyface shiner
Dactylogyrus rubellus (Ont)	
Pimephales notatus (Rafinesque)	bluntnose minnow
Dactylogyrus bifurcatus (Man, Ont)	
D. bychowskyi (Ont)	
Gyrodactyloidea gen. sp. (Ont)	
Pimephales promelas Rafinesque	fathead minnow
Dactylogyrus bifurcatus (Ont)	
D. bychowskyi (Ont)	
Dactylogyrus sp. (Man, Ont)	
Gyrodactylus hoffmani (Ont)	
Octomacrum lanceatum (Ont)	
Platygobio gracilis (Richardson)	flathead chub
Cleidodiscus brachus (Alta)	
Dactylogyrus albertensis (Alta)	
Ptychocheilus oregonensis (Richardson)	northern squawfish
Dactylogyrus columbiensis (BC)	
D. ptychocheilus (BC)	
D. tridactylus (BC)	
D. vancleavei (BC)	
Gyrodactyloidea gen. sp. (BC)	
Rhinichthys atratulus (Hermann)	blacknose dace
Dactylogyrus banghami (Ont)	
D. cheloideus (Ont)	
Gyrodactylus atratuli (Ont)	
G. avalonia (Ont)	
G. dechtiari (Ont)	
G. stunkardi (Ont)	
Rhinichthys cataractae (Valenciennes)	longnose dace
Dactylogyrus banghami (Alta, BC, Man, Ont)	
Gyrodactyloidea gen. sp. (BC)	
Gyrodactylus atratuli (Ont)	
Gyrodactylus cheloideus (Ont)	
G. dechtiari (Ont)	
G. stunkardi (Lab, Ont)	
Richardsonius balteatus (Richardson)	redside shiner
Dactylogyrus banghami (BC)	
D. richardsonius (BC)	
Gyrodactyloidea gen. sp. (BC)	
Octomacrum microconfibula (BC)	
Octomacrum sp. (BC)	
Pellucidhaptor pellucidhaptor (BC)	
Semotilus atromaculatus (Mitchill)	creek chub
Cleidodiscus brachus (NB, Ont)	
Dactylogyrus attenuatus (Ont)	
D. dubius (NB)	
D. microphallus (Ont)	

Dactylogyrus sp. (NB, Ont)
Gyrodactylidae gen. sp. (Ont)
Gyrodactyloidea gen. sp. (Ont)
Gyrodactylus sp. (NB)
Octomacrum semotili (Ont)
Octomacrum sp. (Ont)

Semotilus corporalis (Mitchill) fallfish
Dactylogyrus corporalis (NB)

Semotilus margarita (Cope) pearl dace
Cleidodiscus brachus (NB)
Dactylogyrus sp. (NB)
Octomacrum microconfibula (NB)
O. semotili (Man, Ont)
Octomacrum sp. (Ont)

Family CATOSTOMIDAE

Carpiodes cyprinus (Lesueur) quillback
Acolpenteron catostomi (Ont)
Anonchohaptor anomalum (Man, Ont)
Anonchohaptor sp. (Ont)
Icelanonchohaptor fyviei (Ont)
Neodiscocotyle carpioditis (Ont)
Pellucidhaptor sp. (Ont)

Catostomus catostomus (Forster) longnose sucker
Acolpenteron catostomi (BC, Que)
Anonchohaptor anomalum (BC, Lab, Ont, YT)
Gyrodactyloidea gen. sp. (BC)
Gyrodactylus aquilinus (Lab)
G. atratuli (Lab)
G. spathulatus (Lab)
Monogenea gen. sp. (BC)
Octomacrum lanceatum (BC)
Pellucidhaptor catostomi (Ont)
P. nasalis (BC)
Pseudomurraytrema copulatum (BC)

Catostomus commersoni (Lacépède) white sucker
Acolpenteron catostomi (Man, NB, Ont)
Anonchohaptor anomalum (BC, Lab, Man, NB, Ont)
Dactylogyrus sp. (Ont)
Gyrodactylidae gen. sp. (Ont)
Gyrodactylus commersoni (Lab)
G. spathulatus (Man, Ont)
G. stunkardi (Ont)
Octomacrum lanceatum (Man, Ont)
Pellucidhaptor nasalis (Man, NB, Ont)
Pseudomurraytrema alabarrum (Alta)
P. copulatum (BC, Man, Ont)

Catostomus macrocheilus Girard largescale sucker
Acolpenteron catostomi (BC)
Anonchohaptor anomalum (BC)
Gyrodactyloidea gen. sp. (BC)
Octomacrum lanceatum (BC)
Pseudomurraytrema copulatum (BC)

Hypentelium nigricans (Lesueur) northern hog sucker
Dactylogyrus apos (Ont)

Moxostoma anisurum (Rafinesque) silver redhorse
Anonchohaptor anomalum (Man, Ont)
Dactylogyrus urus (Ont)
Gyrodactylus spathulatus (Man, Ont)
Gyrodactylus sp. (Ont)
Pseudomurraytrema copulatum (Man, Ont)
Pseudomurraytrema sp. (Man, Ont)

Moxostoma erythrurum (Rafinesque) golden redhorse
Anonchohaptor anomalum (Man, Ont)
Dactylogyrus urus (Man, Ont)
Dactylogyrus sp. (Ont)
Pseudomurraytrema copulatum (Ont)
Pseudomurraytrema sp. (Man, Ont)

Moxostoma macrolepidotum (Lesueur) shorthead redhorse
Anonchohaptor anomalum (Ont)
Dactylogyrus sp. (Ont)
Gyrodactylus sp. (Ont)
Pellucidhaptor sp. (Ont)
Pseudomurraytrema copulatum (Ont)
P. moxostomi (*nomen nudum*) (Ont)
Pseudomurraytrema sp. (Ont)

ORDER SILURIFORMES

Family ICTALURIDAE

Ictalurus melas (Rafinesque) black bullhead
Ligictaluridus pricei (Ont)

Ictalurus nebulosus (Lesueur) brown bullhead
Gyrodactylidae gen. sp. (Ont)
Gyrodactyloidea gen. sp. (BC, Ont)
Gyrodactylus nebulosus (Ont)
Ligictaluridus floridanus (Ont)
L. pricei (Man, NB, Ont)

Ictalurus punctatus (Rafinesque) channel catfish
Gyrodactyloidea gen. sp. (Ont)
Ligictaluridus floridanus (Ont)
L. pricei (Ont)

Noturus flavus Rafinesque stonecat
Ligictaluridus pricei (Ont)

Noturus gyrinus (Mitchill) tadpole madtom
Gyrodactylus sp. (Man, Ont)
Ligictaluridus floridanus (Ont)
L. pricei (Ont)

ORDER PERCOPSIFORMES

Family PERCOPSIDAE

Percopsis omiscomaycus (Walbaum) trout-perch
Cleidodiscus sp. (Ont)
Gyrodactyloidea gen. sp. (Ont)
Gyrodactylus sp. (Man, Ont)
Urocleidus baldwini (Ont)

ORDER GADIFORMES

Family MACROURIDAE

- *Macrourus berglax* Lacépède roughhead grenadier
  - *Cyclocotyloides pinguis* (Atl)
  - *Diclidophora* sp. (Atl)
  - *Macruricotyle newfoundlandiae* (Atl)

- *Macrourus rupestris* (Gunnerus) roundnose grenadier
  - *Diclidophora macruri* (Atl)

Family GADIDAE

- *Gadus morhua* Linnaeus Atlantic cod
  - *Gyrodactylus* sp. (Atl)
  - *Udonella caligorum* (Atl)†*

- *Merluccius bilinearis* (Mitchill) silver hake
  - *Anthocotyle merlucii* (Atl)

- *Pollachius virens* (Linnaeus) pollock
  - *Diclidophora denticulata* (Atl)

- *Pheragra chalcogramma* (Pallas) walleye pollock
  - *Entobdella pugetenfis* (Pac)

- *Urophycis chuss* (Walbaum) red hake
  - *Diclidophora maccallumi* (Atl)

ORDER ATHERINIFORMES

Family CYPRINODONTIDAE

- *Fundulus diaphanus* (Lesueur) banded killifish
  - *Fundulotrema prolongis* (Ont)
  - *Gyrodactylus avalonia* (Ont)
  - *Salsuginus angularis* (Nfld, NS, Ont)
  - *S. fundulus* (NB, Ont)

- *Fundulus heteroclitus* (Linnaeus) mummichog
  - *Fundulotrema prolongis* (Nfld)
  - *Gyrodactylus stephanus* (Nfld)
  - *Gyrodactylus* sp. (Atl)
  - *Salsuginus angularis* (Nfld)

Family POECILIIDAE

- *Poecilia reticulata* Peters guppy
  - *Gyrodactylus bullatarudis* (Ont, aquarium)

ORDER GASTEROSTEIFORMES

Family GASTEROSTEIDAE

- *Apeltes quadracus* (Mitchill) fourspine stickleback
  - *Gyrodactylus avalonia* (Nfld-b)
  - *G. cameroni* (Nfld-b)
  - *G. canadensis* (Nfld-b)

- *Culaea inconstans* (Kirtland) brook stickleback
  - *Dactylogyrus eucalius* (Man, Ont)
  - Gyrodactyloidea gen. sp. (BC, Ont)
  - *Gyrodactylus eucaliae* (Man, Ont)
  - *Gyrodactylus* sp. (Ont)

- *Gasterosteus aculeatus* Linnaeus threespine stickleback
  - *Dactylogyrus* sp. (BC)
  - Gyrodactyloidea gen. sp. (Pac, BC)
  - *Gyrodactylus alexanderi* (Pac, BC)
  - *G. avalonia* (Atl, Lab-b, Lab, Nfld-b, Nfld, Ont, Que-b, Que)
  - *G. canadensis* (Atl, Nfld-b, Nfld, Que-b, Que)

- *Gasterosteus wheatlandi* Putnam blackspotted stickleback
  - *Gyrodactylus avalonia* (Nfld-b)

- *Pungitius pungitius* (Linnaeus) ninespine stickleback
  - *Gyrodactylus avalonia* (Lab-b, Nfld, Que-b, Que)
  - *G. canadensis* (Lab-b, Nfld, Que-b, Que)
  - *G. stephanus* (Nfld)
  - *Gyrodactylus* sp. (Alta)

Family SYNGNATHIDAE

- *Syngnathus griseolineatus* Ayres[102] bay pipefish
  - Gyrodactyloidea gen. sp. (Pac)

ORDER PERCIFORMES

Family PERCICHTHYIDAE

- *Morone americana* (Gmelin) white perch
  - *Cleidodiscus* sp. (Ont)
  - *Onchocleidus rogersi* (Ont)

- *Morone chrysops* (Rafinesque) white bass
  - Gyrodactyloidea gen. sp. (Ont)
  - *Onchocleidus chrysops* (Ont)

Family CENTRARCHIDAE

- *Ambloplites rupestris* (Rafinesque) rock bass
  - *Cleidodiscus* sp. (Ont)
  - Gyrodactyloidea gen. sp. (Ont)
  - *Gyrodactylus goerani* (Ont)
  - *Gyrodactylus* sp. (Man, Ont)
  - *Leptocleidus megalonchus* (unspecified locality)
  - *Lyrodiscus minimus* (Ont)
  - *L. rupestris* (Ont)
  - *Onchocleidus chautauquaensis* (Ont)
  - *Tetracleidus glenorensis* (Ont)
  - *T. stentor* (Ont)
  - "*Urocleidus*" *alatus* (Ont)

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[102] *Syngnathus griseolineatus* is treated as a subspecies of *S. leptorhynchus* by Hubbs et al. (1979).

Lepomis gibbosus (Linnaeus) pumpkinseed
Actinocleidus gibbosus (Ont)
A. incus (Ont)
A. oculatus (Ont)
A. recurvatus (NB, Ont)
Cleidodiscus robustus (Ont)
Gyrodactylidae gen. sp. (Ont)
Gyrodactyloidea gen. sp. (BC, Ont)
Gyrodactylus avalonia (Ont)
G. macrochiri (Man, Ont)
Haplocleidus dispar (NB, Ont)
Leptocleidus megalonchus (unspecified locality)
Onchocleidus attenuatus (Ont)
O. ferox (Ont)
O. similis (NB, Ont)
Pterocleidus acer (Ont)

Lepomis macrochirus Rafinesque bluegill
Actinocleidus bakeri (Ont)
A. gibbosus (Ont)
A. unguis (Ont)
Cleidodiscus robustus (Ont)
C. venardi (Ont)
Cleidodiscus sp. (Ont)
Gyrodactyloidea gen. sp. (Ont)
Haplocleidus dispar (Ont)
Lyrodiscus longibasus (Ont)
L. seminolensis (Ont)
Lyrodiscus sp. (Ont)
Onchocleidus ferox (Ont)

Micropterus dolomieui Lacépède smallmouth bass
Actinocleidus fusiformis (Man, Ont)
Ancyrocephalidae[103] sp. (NS)
Cleidodiscus sp. (Ont)
Dactylogyrus extensus (NS)
Gyrodactylidae gen. sp. (Ont)
Gyrodactyloidea gen. sp. (Ont)
Gyrodactylus macrochiri (Ont)
Gyrodactylus[104] sp. (Ont)
Haplocleidus dispar (Ont)
Leptocleidus megalonchus (Ont)
Onchocleidus ferox (Ont)
O. principalis (Ont)
Tetracleidus banghami (Man, Ont)
T. glenorensis (Ont)

Micropterus salmoides (Lacépède) largemouth bass
Actinocleidus fusiformis (Ont)
A. mizellei (Ont)
Gyrodactyloidea gen. sp. (BC, Ont)
Gyrodactylus macrochiri (Ont)
Haplocleidus dispar (Ont)
H. furcatus (Ont)
Onchocleidus helicis (Ont)
O. principalis (Ont)
?*Urocleidus* sp. (Ont)

Pomoxis annularis Rafinesque white crappie
Lyrodiscus longibasus (Ont)
Tetracleidus capax (Ont)
T. longus (Ont)

Pomoxis nigromaculatus (Lesueur) black crappie
"*Cleidodiscus*" *vancleavei* (Ont)
Gyrodactyloidea gen. sp. (BC, Ont)
Lyrodiscus longibasus (Ont)
Lyrodiscus sp. (Ont)
Tetracleidus capax (Man, Ont)
Tetracleidus longus (Ont)

Family PERCIDAE

Etheostoma caeruleum Storer rainbow darter
Aethycteron caerulei (Ont)

Etheostoma exile (Girard) Iowa darter
Gyrodactylus etheostomae (Ont)
Gyrodactylus sp. (Man, Ont)

Etheostoma flabellare Rafinesque fantail darter
Aethycteron moorei (Ont)

Etheostoma microperca Jordan and Gilbert least darter
Aethycteron micropercae (Ont)

Etheostoma nigrum Rafinesque johnny darter
Aethycteron hargisi (Ont)
A. nigrei (Ont)
Gyrodactyloidea gen. sp. (Ont)
Gyrodactylus etheostomae (Ont)
G. stunkardi (Ont)
Gyrodactylus sp. (Man, Ont)

Perca flavescens (Mitchill) yellow perch
Cleidodiscus sp. (Ont)
Gyrodactylidae gen. sp. (Ont)
Gyrodactyloidea gen. sp. (Ont)
Gyrodactylus freemani (Ont)
Urocleidus adspectus (Man, NB, Ont)

Percina caprodes (Rafinesque) logperch
Aethycteron malleus (Man, Ont)
Gyrodactyloidea gen. sp. (Ont)

Percina maculata (Girard) blackside darter
Aethycteron malleus (Ont)

Stizostedion canadense (Smith) sauger
Urocleidus aculeatus (Man, Ont)

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[103] "*Ancyrocephalus*" sp. of Fantham and Porter (1948) — see the records of ancyrocephalid species of uncertain generic affinity on p. 62.

[104] See footnote 61.

Stizostedion vitreum glaucum Hubbs	blue pike
Urocleidus aculeatus (Ont)	
Stizostedion vitreum vitreum (Mitchill)	walleye
Cleidodiscus sp. (Ont)	
Gyrodactyloidea gen. sp. (Ont)	
Urocleidus aculeatus (Man, Ont)	
Family SCIAENIDAE	
Aplodinotus grunniens Rafinesque	freshwater drum
Lintaxine cokeri (Ont)	
Microcotyle eriensis (Ont)	
M. spinicirrus (Ont)	
Family EMBIOTOCIDAE	
Cymatogaster aggregata Gibbons	shiner perch
Gyrodactyloidea gen. sp. (Pac)	
Gyrodactylus sp. (Pac)	
Family LABRIDAE	
Tautogolabrus adspersus (Walbaum)	cunner
Gyrodactylus adspersi (Atl)	
Family PHOLIDAE	
Pholis ornata (Girard)	saddleback gunnel
Gyrodactyloidea gen. sp. (Pac)	
Family AMMODYTIDAE	
Ammodytes hexapterus Pallas	Pacific sand lance
Gyrodactyloidea gen. sp. (Pac)	
Family SCOMBRIDAE	
Scomber scombrus Linnaeus	Atlantic mackerel
Kuhnia scombri (Atl)	
Family XIPHIIDAE	
Xiphias gladius Linnaeus	swordfish
Tristoma coccineum (Atl)	
T. integrum (Atl)	
Family STROMATEIDAE	
Peprilus triacanthus (Peck)	butterfish
Microcotyle poronoti (Atl)	
Family SCORPAENIDAE	
Sebastes aleutianus (Jordan and Evermann)	rougheye rockfish
Trochopus sp. (Pac)	
Sebastes alutus (Gilbert)	Pacific ocean perch
Microcotyle sebastis (Pac)	
Microcotyle sp. (Pac)	
Pseudacanthocotyla williamsi (Pac)**	
Trochopus marginata (Pac)	
Trochopus sp. (Pac)	
Sebastes babcocki (Thompson)	redbanded rockfish
Trochopus sp. (Pac)	
Sebastes borealis Barsukov	shortraker rockfish
Trochopus sp. (Pac)	
Sebastes brevispinis (Bean)	silvergray rockfish
Microcotyle sebastis (Pac)	
Trochopus sp. (Pac)	
Sebastes caurinus Richardson	copper rockfish
Microcotyle sebastis (Pac)	
Microcotyle sp. (Pac)	
Trochopus marginata (Pac)	
T. trituba (Pac)	
Sebastes crameri (Jordan)	darkblotched rockfish
Benedenia derzhavini (Pac)	
Trochopus sp. (Pac)	
Sebastes diploproa (Gilbert)	splitnose rockfish
Microcotyle sebastis (Pac)	
Trochopus sp. (Pac)	
Sebastes elongatus Ayres	greenstriped rockfish
Microcotyle sebastis (Pac)	
Trochopus sp. (Pac)	
Sebastes entomelas (Jordan and Gilbert)	widow rockfish
Trochopus sp. (Pac)	
Sebastes flavidus (Ayres)	yellowtail rockfish
Trochopus sp. (Pac)	
Sebastes goodei (Eigenmann and Eigenmann)	chilipepper
Trochopus sp. (Pac)	
Sebastes helvomaculatus Ayres	rosethorn rockfish
Microcotyle sebastis (Pac)	
Sebastes maliger (Jordan and Gilbert)	quillback rockfish
Microcotyle sebastis (Pac)	
Trochopus marginata (Pac)	
Sebastes nebulosus Ayres	China rockfish
Trochopus marginata (Pac)	
Sebastes nigrocinctus Ayres	tiger rockfish
Microcotyle sebastis (Pac)	
Sebastes paucispinis Ayres	bocaccio
Microcotyle sebastis (Pac)	

Sebastes pinniger (Gill) canary rockfish
Trochopus trituba (Pac)
Trochopus sp. (Pac)

Sebastes proriger (Jordan and Gilbert redstripe rockfish
Benedenia derzhavini (Pac)
Microcotyle sebastis (Pac)
Trochopus sp. (Pac)

Sebastes reedi (Westrheim and Tsuyuki) yellowmouth rockfish
Benedenia derzhavini (Pac)
Microcotyle sebastis (Pac)
Trochopus sp. (Pac)

Sebastes ruberrimus (Cramer) yelloweye rockfish
Trochopus sp. (Pac)

Sebastes variegatus Quast harlequin rockfish
Benedenia derzhavini (Pac)
Microcotyle sebastis (Pac)

Sebastes wilsoni (Gilbert) pygmy rockfish
Microcotyle sebastis (Pac)

Sebastes zacentrus (Gilbert) sharpchin rockfish
Benedenia derzhavini (Pac)
Microcotyle sebastis (Pac)
Trochopus sp. (Pac)

Family HEXAGRAMMIDAE

Hexagrammos lagocephalus (Pallas) rock greenling
Microcotyle sebastis (Pac)

Family COTTIDAE

Cottus asper Richardson prickly sculpin
Gyrodactyloidea gen. sp. (BC)

Cottus bairdi Girard mottled sculpin
Dactylogyrus buddi (Ont)
Dactylogyrus sp. (Man, Ont)
Gyrodactylus bairdi (Lab, Man, Ont)
G. lacusgrandis (Lab)

Cottus cognatus Richardson slimy sculpin
Dactylogyrus buddi (Ont, YT)
Gyrodactyloidea gen. sp. (BC)
Gyrodactylus bairdi (YT)

Cottus rhotheus (Smith) torrent sculpin
Gyrodactyloidea gen. sp. (BC)

Myoxocephalus quadricornis (Linnaeus) fourhorn sculpin
Gyrodactylus nainum (Lab-b)

Myoxocephalus scorpius (Linnaeus) shorthorn sculpin
Gyrodactylus groenlandicus (Atl)

Oligocottus maculosus Girard tidepool sculpin
Gyrodactyloidea gen. sp. (Pac)

ORDER PLEURONECTIFORMES

Family PLEURONECTIDAE

Atheresthes stomias (Jordan and Gilbert) arrowtooth flounder
Entobdella pugetensis (Pac)

Hippoglossus hippoglossus (Linnaeus) Atlantic halibut
Entobdella curvunca (Atl)
E. hippoglossi (Atl)
Udonella caligorum (Atl)†*

Hippoglossus stenolepis Schmidt Pacific halibut
Entobdella hippoglossi (Pac)

Platichthys stellatus (Pallas) starry flounder
Gyrodactyloidea gen. sp. (Pac)

Pleuronectidae gen. sp.
Entobdella sp. (Pac)

Pseudopleuronectes americanus (Walbaum) winter flounder
Gyrodactylus pleuronecti (Atl, Nfld-b)

Reinhardtius hippoglossoides (Walbaum) Greenland turbot
Entobdella hippoglossi (Atl)

ORDER TETRAODONTIFORMES

Family MOLIDAE

Mola mola (Linnaeus) ocean sunfish
Capsala martinierei (Atl, Pac)

SUMMARY

Keys, diagnoses, morphometric data, figures, and records are provided for the Monogenea and Turbellaria found on fishes of Canada up to the end of 1983. The following new or emended taxonomic proposals, listed in order of appearance in the text, are included: *Actinocleidus scapularis* Mizelle and Donahue, 1944 and *A. sigmoideus* Mizelle and Donahue, 1944 are synonymized with *A. incus* Mizelle and Donahue, 1944; *Ligictaluridus* n. g. is proposed for two ancyrocephalids from Ictaluridae — *L. pricei* (Mueller, 1936) n. comb. (syn. *Cleidodiscus pricei* Mueller, 1936) as type species and *L. floridanus* (Mueller, 1936) n. comb. (syn. *Cleidodiscus floridanus* Mueller, 1936); *Urocleidus procax* Mizelle and Donahue, 1944 is synonymized with *O. similis* Mueller, 1936; *Onchocleidus chrysops* (Mizelle and Klucka, 1953) n. comb. for *Urocleidus chrysops* Mizelle and Klucka, 1953; *Onchocleidus attenuatus* (Mizelle, 1941) n. comb. for *Urocleidus attenuatus* Mizelle, 1941; *Onchocleidus rogersi* (Hanek and Fernando, 1972) n. comb. for *Urocleidus rogersi* Hanek and Fernando, 1972; *Onchocleidus helicis* Mueller, 1936 is reinstated (syn. *Urocleidus helicis* (Mueller, 1936) Mizelle and Hughes, 1938); *Onchocleidus principalis* Mizelle, 1936 is reinstated (syn. *Urocleidus principalis* (Mizelle, 1936) Mizelle and Hughes, 1938); *Salsuginus* n. g. is proposed for two ancyrocephalids from Cyprinodontidae (*Fundulus* spp.) — *S. angularis* (Mueller, 1934) n. comb. (syn. *Urocleidus angularis* Mueller, 1934) as type species and *S. fundulus* (Mizelle, 1940) n. comb. (syn. *Urocleidus fundulus* Mizelle, 1940); *Tetracleidus stentor* (Mueller, 1937) n. comb. for *Cleidodiscus stentor* Mueller, 1937; *Tetracleidus capax* (Mizelle, 1936) n. comb. for *Cleidodiscus capax* Mizelle, 1936; *Tetracleidus glenorensis* (Hanek and Fernando, 1972) n. comb. for *Cleidodiscus glenorensis* Hanek and Fernando, 1972; *Tetracleidus longus* (Mizelle, 1936) n. comb. for *Cleidodiscus longus* Mizelle, 1936; *Cleidodiscus uniformis* Mizelle, 1936 is synonymized with *Tetracleidus longus* (Mizelle, 1936) n. comb.; *Urocleidus baldwini* (Dechtiar, 1974) n. comb. for *Cleidodiscus baldwini* Dechtiar, 1974; the following, listed by Margolis and Arthur (1979), are regarded as *incertae sedis*: "*Ancyrocephalus*" sp., "*Cleidodiscus*" *vancleavei* Mizelle, 1936; "*Urocleidus*" *alatus* (Mueller, 1938) Price, 1968; Pseudomurraytrematinae Kritsky, Mizelle and Bilqees, 1978 is elevated to Pseudomurraytrematidae; *Pseudomurraytrema muelleri* Price, 1967 is synonymized with *P. alabarrum* Rogers, 1966 (Rogers, pers. comm.); *Gyrodactylus lairdi* Hanek and Threlfall, 1969, *G. memorialis* Hanek and Threlfall, 1969, and *G. terranovae* Hanek and Threlfall, 1969 are synonymized with *G. avalonia* Hanek and Threlfall, 1969.

Following Margolis and Arthur (1979) the suborder Polyopisthocotylea Odhner, 1912 is regarded as an order for which the ordinal suffix "ida" is utilized. Superfamilies within the Polyopisthocotylida are designated as Diclybothrioidea (=Diclybothriidea Bykhovsky, 1957, order) status emended; Hexabothrioidea (="hexabothriid" sensu Llewellyn 1970) status emended; Mazocraeoidea (=Mazocraeidea Bykhovsky, 1957, order) status emended.

A new host record is *Octomacrum lanceatum* Mueller, 1934 on *Pimephales promelas* (Ont.).

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APPENDICES

Appendix 1. Classification of the Turbellaria and Monogenea Recorded from Fishes of Canada.

TURBELLARIA(i) — Neoophora

ORDER SERIATA Westblad, 1935 (suborder Tricladida)

- Procerodidae Diesing, 1862
  - *Micropharynx* (M)

ORDER UDONELLIDA Ivanov and Mamkaev, 1973 (= Udonellidae van Beneden and Hesse, 1863)

- *Udonella* (M)

MONOGENEA

- Microbothriidae Price, 1936 (M)
  - *Microbothrium* (M)

ORDER DACTYLOGYRIDA(ii) Bykhovsky, 1937 (M, FW, BW)

- Acanthocotylidae Price, 1936 (M)
  - *Pseudacanthocotyla* (M)

- Ancyrocephalidae (Bykhovsky, 1937, subfam.) Bykhovsky and Nagibina, 1978 (FW, BW)
  - *Actinocleidus*(iii) (FW)
  - *Aethycteron* (FW)
  - *Cleidodiscus* (FW)
  - *Haplocleidus* (FW)
  - *Leptocleidus* (FW)
  - *Ligictaluridus* (FW)
  - *Lyrodiscus* (FW)
  - *Onchocleidus* (FW)
  - *Pterocleidus* (FW)
  - *Salsuginus* (FW, BW)
  - *Tetracleidus* (FW)
  - *Urocleidus* (FW)

- Capsalidae Baird, 1853 (M,BW)
  - *Benedenia* (M)
  - *Capsala* (M)
  - *Entobdella* (M)
  - *Nitzschia* (BW)
  - *Tristoma* (M)
  - *Trochopus* (M)

- Dactylogyridae Bykhovsky, 1933 (FW)
  - *Acolpenteron*
  - *Dactylogyrus*
  - *Pellucidhaptor*
  - *Pseudacolpenteron*

- Pseudomurraytrematidae (Kritsky, Mizelle and Bilqees, 1978, subfam.) status emend. (FW)
  - *Anonchohaptor*
  - *Icelanonchohaptor*
  - *Pseudomurraytrema*

- Tetraonchidae Bykhovsky, 1937 (FW)
  - *Tetraonchus*

ORDER GYRODACTYLIDA Bykhovsky, 1937 (M,FW, BW)

- Gyrodactylidae Cobbold, 1864 (M, FW, BW)
  - *Fundulotrema* (FW)
  - *Gyrodactyloides* (M)
  - *Gyrodactylus* (M,FW,BW)
  - *Laminiscus* (M)

ORDER POLYOPISTHOCOTYLIDA(iv) (Odhner, 1912, suborder) status emend. (M,FW,BW)

- Diclybothrioidea(v) (Bykhovsky, 1957, order) status emend. (FW,BW)
  - Diclybothriidae Bykhovsky and Gusev, 1950 (FW)
    - *Diclybothrium*
    - *Paradiclybothrium*

- Hexabothrioidea (="hexabothriid" sensu Llewellyn, 1970) status emend. (M)

(i) Classification of the Turbellaria based on that of Ivanov and Mamkaev (1973).

(ii) In order to standardize ordinal suffixes (ida) the spelling has been emended as necessary e.g. Dactylogyridea of Bykhovsky (1937) becomes Dactylogyrida.

(iii) Within each family the genera are listed alphabetically.

(iv) Recognizing the Monogenea as a distinct class within the phylum Platyhelminthes (rather than an order of the Trematoda), Margolis and Arthur (1979) regarded the Polyopisthocotylea as an order which Llewellyn (pers. comm., 1981) considered to be of equal rank with the Dactylogyrida and Gyrodactylida. Thus, the ordinal suffix (ida) is used for this group which was originally proposed by Odhner (1912) as a suborder (Polyopisthocotylea) of the Monogenea.

(v) Superfamilies are utilized for the polyopisthocotylidan worms as it is convenient to group the families which can be included in the taxon herein designated as the Mazocraeoidea. The suffixes for the taxa proposed by Bykhovsky (1957) at the ordinal level (Diclybothriidea and Mazocraeidea (spelled in error on p. 402 of A.I.B.S. translation as Mazocraeidae)) are herein emended to denote superfamilial rank.

Hexabothriidae Price, 1942 (M)
Rajonchocotyle
Squalonchocotyle

Mazocraeoidea (Bykhovsky, 1957, order) status emend. (M,FW)

Anthocotylidae Bykhovsky, 1957 (M)
Anthocotyle

Diclidophoridae Fuhrmann, 1928 (M)
Cyclocotyloides
Diclidophora
Macruricotyle

Discocotylidae Price 1936 (FW)
Discocotyle
Neodiscocotyle
Octomacrum

Heteraxinidae Price, 1962 (FW)
Lintaxine

Mazocraeidae Price, 1936 (M,FW)
Kuhnia (M)
Mazocraeoides (FW)
Pseudomazocraeoides (FW)

Microcotylidae Taschenberg, 1897 (M,FW)
Microcotyle (M,FW)

Appendix 2. Evolution Within the Monogenea(1) (after Llewellyn, 1970).

A "protomonogenean" ancestor may have evolved from a rhabdocoel-like turbellarian by remaining in continuous contact while feeding on the epidermis of relatively large prey animals (which were presumed to be early vertebrates). Contact may have been maintained by means of the muscular action of the posterior body region which, as the prey animals evolved towards a fast-swimming way of life, developed into a discrete disc or "haptor". At this stage the udonellids may have diverged leaving the main monogenean stock which developed a more sophisticated "octodiametric" attachment organ with 16 radially arranged, ventrally directed, marginal hooks (Appendix 2, Fig. 1). Perhaps a microbothriid ancestor became associated with protoelasmobranch hosts and, instead of attaching to the host epidermis, became cemented to the placoid scales. The marginal hooks would thus become redundant and, subsequently, be lost. However, vestiges of marginal hooks occur temporarily in the larvae of at least some extant microbothriids (Kearn 1965).

The main monogenean stock, with it's "octodiametric" haptor, persisted as skin parasites and developed a pair of relatively heavy-duty hooks or hamuli, one on each side of the haptor in the space between marginal hooks II and III (Appendix 2, Fig. 2A). These parasites would be oriented with the haptor "upstream" to the waterflow produced by the swimming fish, and the posteriorly positioned hamuli would, therefore, be in the best possible position for optimum attachment. From this ancestral form (Appendix 2, Fig. 2A) two lines may have arisen: in one line, which gave rise to the Dactylogyrida, the posteriormost pair of marginal hooks (I) migrated to the central part of the haptor (Appendix 2, Fig. 2C, 3A); in the other, marginal hooks I remained in the posterior position. The latter line (Appendix 2, Fig. 2B) in turn gave rise to two branches, one of which became viviparous, and gave rise to the Gyrodactylida (Appendix 2, Fig. 2D), while the other remained oviparous. The oviparous branch produced two subbranches, the "monocotylids" and the Polyopisthocotylida (Appendix 2, Fig. 2E, 4A), each of which has conspicuous haptoral modifications. The "monocotylids" have no Canadian representatives and are not discussed further. In the Polyopisthocotylida the oncomiracidia have retained 16 marginal hooks but in the adult some of the pairs of marginal hooks immediately anterior to the hamuli (III, IV, V and usually VI) become replaced by suckers or clamps.

EVOLUTION WITHIN THE DACTYLOGYRIDA

The anterior migration of marginal hooks pair I to the central region of the haptor in the ancestral dactylogyridan (Appendix 2, Fig. 3A) is evident in all the taxa included in the Dactylogyrida. It should be noted that this taxon is not identical with the Dactylogyridea of Bykhovsky, 1957 as Llewellyn (1970) excluded the "monocotylids" and included the "tetraonchoidideans".

The Dactylogyrida evolved along two separate lines: in one group, although the oncomiracidial haptor persisted, the hamuli did not develop and attachment to the host was achieved by a new, larger

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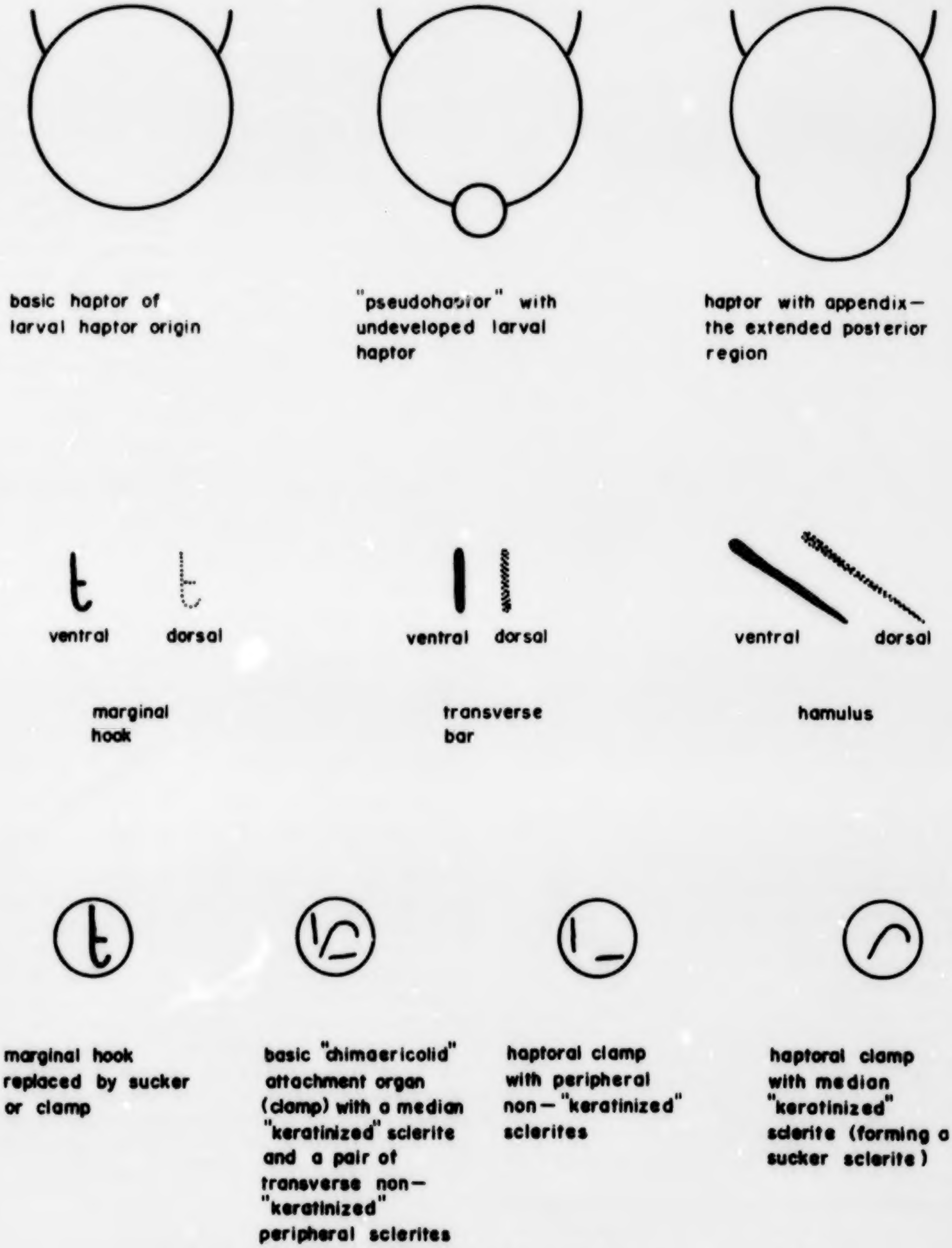
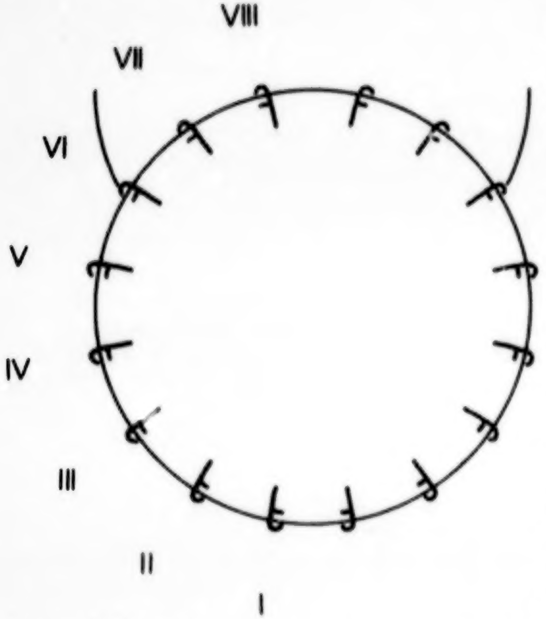
(1)Taxa which have no representatives parasitizing Canadian fishes are not conside· ·1.


basic haptor of larval haptor origin
"pseudohaptor" with undeveloped larval haptor
haptor with appendix— the extended posterior region
ventral
dorsal
marginal hook
ventral
dorsal
transverse bar
ventral
dorsal
hamulus
marginal hook replaced by sucker or clamp
basic "chimaericolid" attachment organ (clamp) with a median "keratinized" sclerite and a pair of transverse non— "keratinized" peripheral sclerites
haptoral clamp with peripheral non— "keratinized" sclerites
haptoral clamp with median "keratinized" sclerite (forming a sucker sclerite)

Explanation of components of Appendix 2, Fig. 1-4.



Appendix 2, Fig. 1. Ancestral "octodiametric" haptor of main monogenean stock.

structure or pseudohaptor (Appendix 2, Fig. 3B) which is typical of the Acanthocotylidae; in the other, the larval haptor persists and develops as the attachment structure. In turn, the latter group (Appendix 2, Fig. 3C) gave rise to two lines: the "protodionchids" which retained the ancestral type of haptoral elaboration and the "mainstream" dactylogyridans in which the hamuli were supported by a transverse bar.

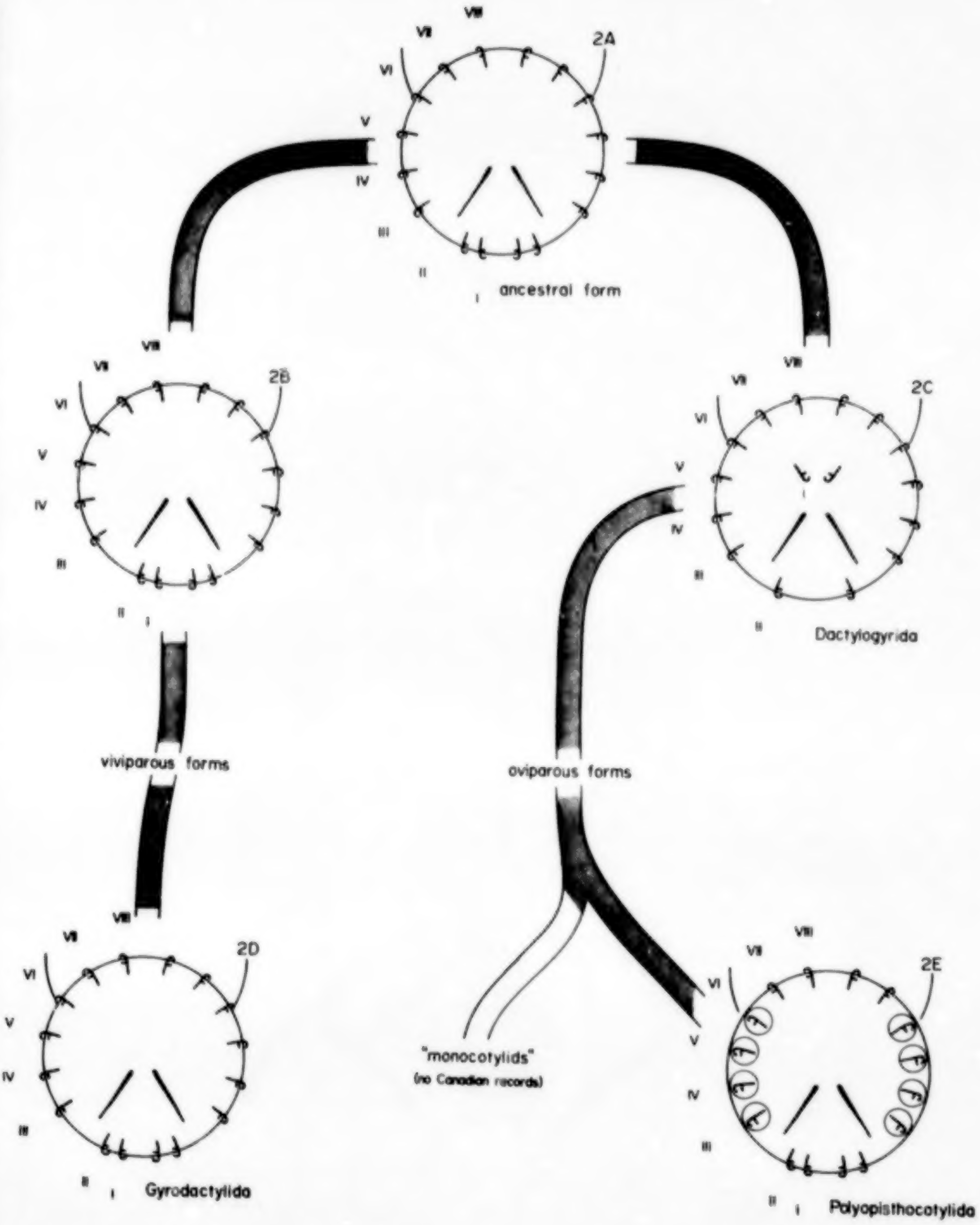
The "protodionchids" gave rise to the "dionchids" (which have no Canadian representatives and are not discussed further) and the Capsalidae (Appendix 2, Fig. 3D) in which two new hamuli appeared, one on each side, just exterior to the original hamuli. In present day capsalids various haptoral modifications exist including the presence of muscular loculi or the development of accessory sclerites derived from the hooks of the centrally placed marginal hooks I. In some capsalid genera, e.g. *Capsala*, the hamuli fail to develop although accessory sclerites may or may not be present.

The mainstream dactylogyridan, with 14 peripheral plus one pair of central marginal hooks and two hamuli supported by a transverse bar, was also characterized by a male copulatory complex comprising a slender, sclerotized, tubular penis which was usually supported by an accessory structure(s). From this group there arose two lines: the "calceostomatids" (which have no Canadian representative and are not further considered) and a group of Monogenea in which a second pair of hamuli appeared which were oriented dorsally. This modification enabled the parasites to attach to the opposing surfaces of adjacent secondary gill lamellae. There is evidence that these hamuli arose ventrally and then migrated to the dorsal surface carrying marginal hooks III and IV with them. This type of haptor (Appendix 2, Fig. 3E) is seen in extant Monogenea such as the tetraonchids, which are parasites of teleosts, and the amphibdellatids, which occur on elasmobranchs. However, the latter are not known from Canadian fishes and are not considered further.

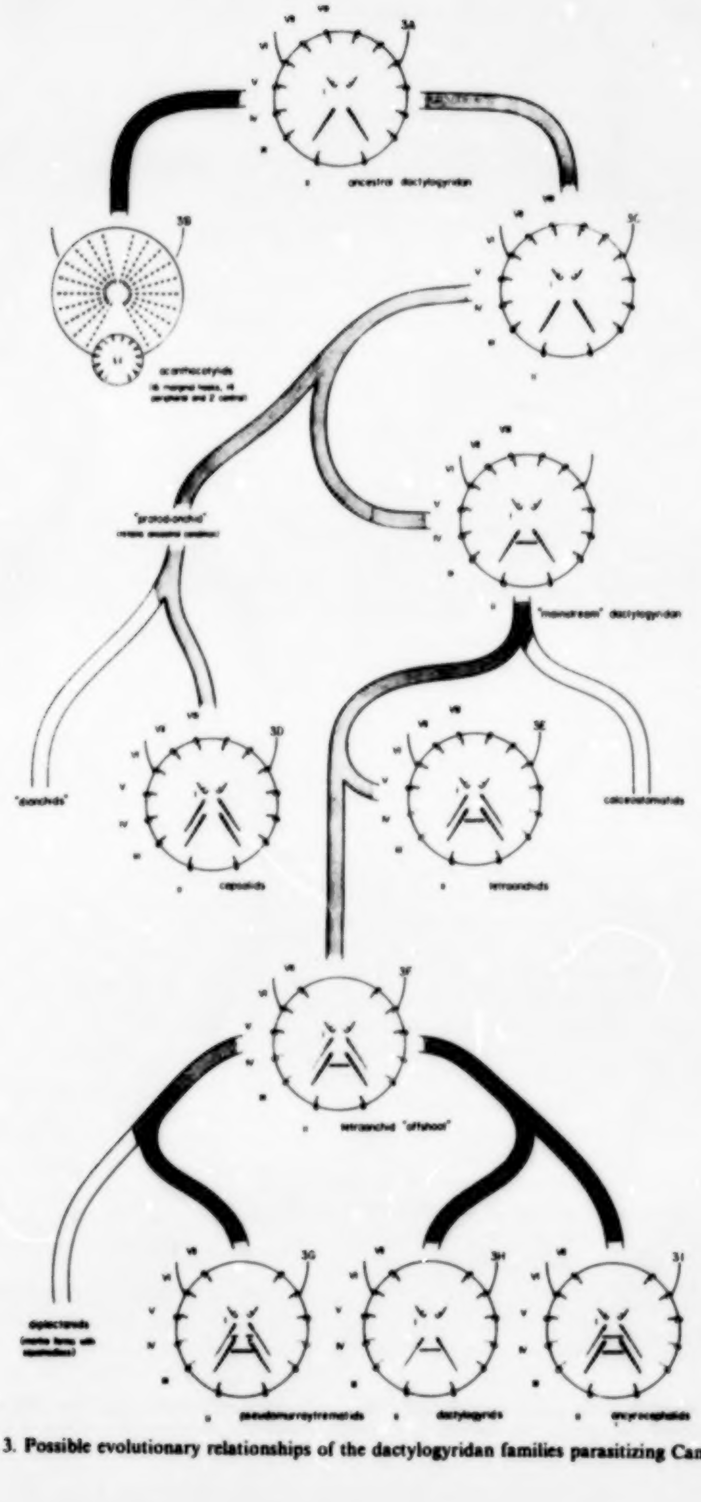
An offshoot from the tetraonchid line lost the anterior pair of peripheral marginal hooks (VIII) so that the total number was reduced to 14: pair I was central in position, pair II was situated between the ventral hamuli, on the posterior margin, and pairs III–VII were peripheral, lying anterior to the hamuli (Appendix 2, Fig. 3F). Part of this line persisted on marine teleosts and developed into the modern diplectanids which, characteristically, have more than two transverse bars as well as supplementary adhesive structures, such as squamodiscs. No diplectanids have been found on Canadian fishes but it is interesting to note that the pseudomurraytrematids, which typically parasitize freshwater fishes (Catostomids), resemble the diplectanids in having an ovary looping the right intestinal caecum and, in some genera where hamuli are present, the dorsal bar is in two parts (Appendix 2, Fig. 3G). Thus the pseudomurraytrematids and diplectanids may have arisen from a common stock, as the looping ovary and presence of more than two bars may be indicative of a phylogenetic relationship. The remainder of the offshoot tetraonchid line (Appendix 2, Fig. 3F) evolved on their freshwater teleost hosts to produce the Ancyrocephalidae, with two pairs of hamuli (one dorsal and one ventral) each with a transverse bar (Appendix 2, Fig. 3I). It is suggested the Dactylogyridae (Appendix 2, Fig. 3H) may have evolved from an ancyrocephalid-like ancestor by reduction of the ventral hamuli and bar which, in dactylogyrids, are vestigial (or lacking). Both the Ancyrocephalidae and Dactylogyridae are characterized by a nonlooping ovary and a vas deferens which encircles the left intestinal caecum and this may, in the present context, be significant.

EVOLUTION WITHIN THE POLYOPISTHOCOTYLIDA

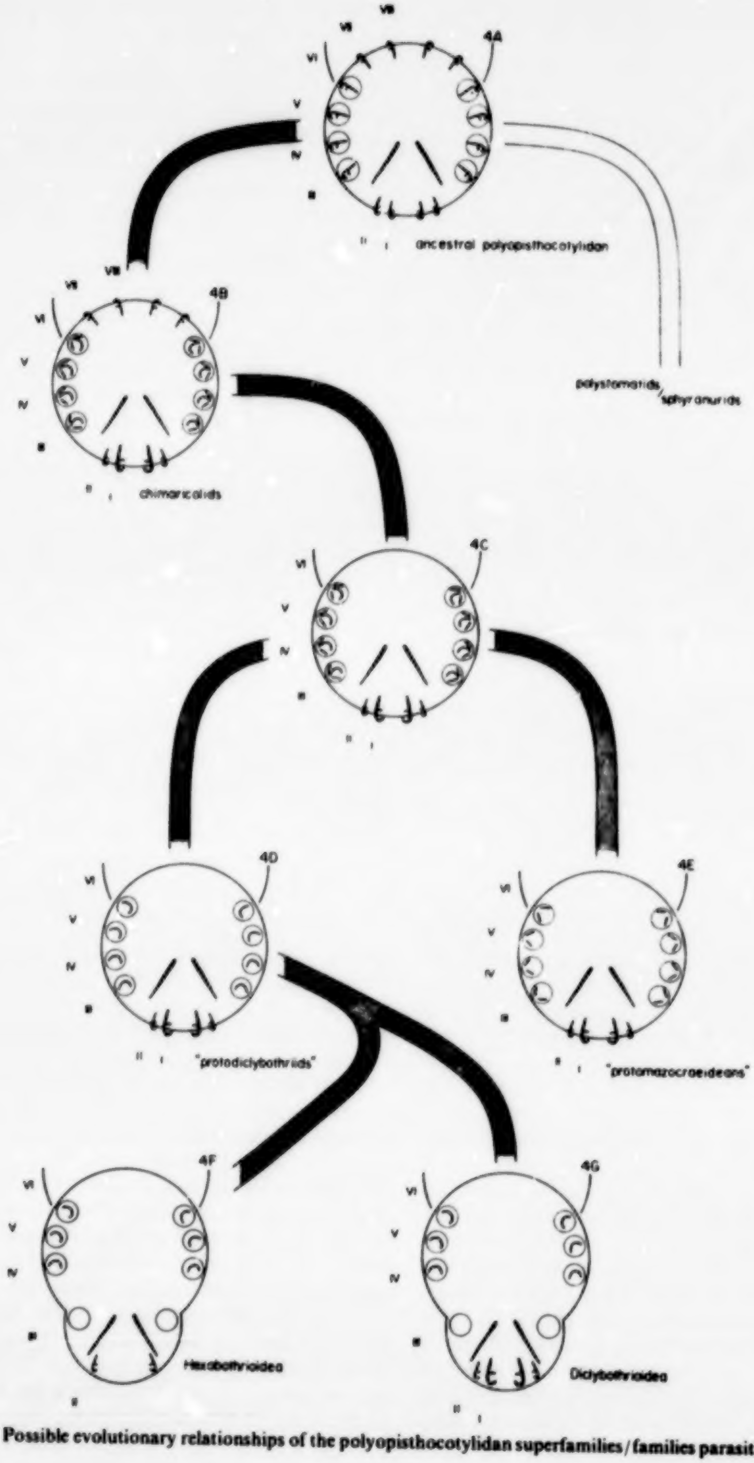
The polyopisthocotylidan haptor has, characteristically, retained 16 marginal hooks, all of which


2A
VIII
VII
VI
V
IV
III
II
I
ancestral form
2B
viviparous forms
2C
Dactylogyrida
oviparous forms
2D
Gyrodactylida
"monocotylids"
(no Canadian records)
2E
Polyopisthocotylida

Appendix 2, Fig. 2. Possible evolutionary relationships of the major monogenean taxa (orders) parasitizing Canadian fishes.


3A
ancestral dactylogyridan
3B
acanthocotylids
3C
"protoonchid"
"mainstream" dactylogyridan
"dionchids"
3D
capsalids
3E
tetraonchids
calceostomatids
3F
tetraonchid "offshoot"
diplectanids
3G
3H
3I
pseudomurraytrematids
dactylogyrids
ancyrocephalids

Appendix 2, Fig. 3. Possible evolutionary relationships of the dactylogyridan families parasitizing Canadian fishes.


4A
VIII
VII
VI
V
IV
III
II
I
ancestral polyopisthocotylidan
polystomatids/sphyranurids
4B
chimaericolids
4C
4D
"protodiclybothriids"
4E
"protomazocraeideans"
4F
Hexabothrioidea
4G
Diclybothrioidea

Appendix 2, Fig. 4. Possible evolutionary relationships of the polyopisthocotylidan superfamilies/families parasitizing Canadian fishes.

remain peripheral so that two pairs (I and II) lie between the single pair of hamuli (Appendix 2, Fig. 4A). In the adults, some of the marginal hooks, immediately anterior to the hamuli, become replaced by a sucker or clamp to provide a more powerful attachment apparatus. As a group, polyopisthocotylidans are blood-feeding leading to modifications of the mouth region and the development of two special ducts: the genito-intestinal canal and the bucco-oesophageal canal.

Each major piscine group has its own characteristic polyopisthocotylidan parasites, indicating major divergences occurred concurrently with the evolution of the host taxa in the Ordovician and Silurian. As a generalization, adaptive radiation in the polyopisthocotylidans developed two types of attachment organs: suckers in the skin-dwelling forms (which eventually evolved to the polystomatids and sphyranurids, almost none of which are parasites of fishes and are therefore not discussed further) and other attachment structures in the gill parasites, which produced the chimaericolid-hexabothriid-diclybothriid-mazocraeidean evolutionary branch.

In this latter group of Monogenea the chimaericolids characteristically had four pairs of gill-gripping organs (Appendix 2, Fig. 4B) each of which has two types of skeletal components: a median, "keratinized", bar and a pair of transverse, nonkeratinized, peripheral sclerites. The 16 marginal hooks were retained but marginal hooks I lost the domus and became enlarged.

Early in their evolution the chimaericolids gave off a branch lacking marginal hooks pairs VII and VIII, with pair I enlarged and lacking the domus, and one pair of hamuli (Appendix 2, Fig. 4C). This branch divided into two stocks: those with a persistent median, keratinized sclerite but lacking the peripheral sclerites, and those lacking the median sclerite but with persistent (nonkeratinized) peripheral sclerites — the "protodiclybothriids" (Appendix 2, Fig. 4D) and protomazocraeideans (Appendix 2, Fig. 4E), respectively.

The protodiclybothriids parasitized a group of hosts which were ancestral to the elasmobranchs and actinopterygians and, as these host taxa underwent adaptive radiation, the parasites also diverged. In the hexabothrioids (Appendix 2, Fig. 4F), which remained on elasmobranchs, the larvae lacked pair I marginal hooks so that the haptor carried only 10 hooks and developed six (rather than eight) haptoral suckers each, supported by a median (keratinized) sucker sclerite: the hamuli were incorporated into the caudal appendix, which also carried a pair of small suckers lacking a median sucker sclerite. The diclybothrioids (Appendix 2, Fig. 4G) evolved on the host stock giving rise to the actinopterygians and some species still parasitize extant modern chondrosteans. In these, pair I marginal hooks persist.

Llewellyn (1970) noted that in the evolution of the haptors of the various descendants of the original protomazocraeidean stock (Appendix 2, Fig. 4E) there have been only relatively minor developments in sclerite arrangement. As noted above, the peripheral (nonkeratinized) sclerites of the chimaericolid-ancestor have been retained, but the median (keratinized) sclerite has been lost although, in the more highly evolved mazocraeideans, a *new* median sclerite (nonkeratinized) has developed. For commentary on the relationships of the mazocraeidean families the reader is referred back to Llewellyn (1970).

Appendix 3. Notes on the systematic positions of *Udonella* and the Microbothriidae.

Order Udonellida Ivanov and Mamkaev, 1973

(=Udonellidae van Beneden and Hesse, 1863)

The systematic position of *Udonella* Johnston, 1835 has been controversial and Nichols (1975) has provided a brief historical review. *Udonella caligorum* Johnston, 1835, was consistently regarded as a monogenean until Ivanov (1952) proposed a separate class to accommodate it. Bykhovsky (1957) supported this proposal and did not include *Udonella* in his monograph on the Monogenea. Llewellyn (1970) speculated that a "protomonogenean", which had evolved from a rhabdocoel turbellarian ancestor, might have given rise to the "udonellids" as well as the main monogenean stock but avoided comment on the taxonomic affinities of *Udonella* with extant forms. More recently Ivanov and Mamkaev (1973) suggested a new order, the Udonellida, should be included with the neoophoran Turbellaria and this is accepted by the present author. It is of interest that Nichols (1975) was not able to clarify the phylogenetic position of *Udonella* but was, apparently, unaware of Ivanov and Mamkaev's paper.

Microbothriidae Price, 1936

Although the Microbothriidae have generally been regarded as Monogenea, Bykhovsky (1957) suggested a possible relationship with the rhabdocoel turbellarians. In order to resolve this problem, Kearn (1965) studied the larvae of *Leptocotyle minor*, a microbothriid which attaches to the placoid scales of dogfish, and found six marginal "spicules" which were thought to be possible homologues of the marginal hooks of other Monogenea. Llewellyn (1970) considered the microbothriids had evolved from an early monogenean stock which parasitized a vertebrate line that led, eventually, to the elasmobranchs and were distinct from the "dactylogyrideans" which included the Capsalidae. Later, Llewellyn (pers. comm. 1981) suggested the microbothrioideans may be "degenerate" monocotyloideans.(1)

The present author concludes that the Microbothriidae should be regarded as a monogenean family but, as there is still speculation concerning its affinities, an assignment to a higher taxon has not been attempted. Familial diagnoses were provided by Dawes (1946), Sproston (1946), Bykhovsky (1957), and Yamaguti (1963) but vary depending on presumed relationships.

Appendix 4. Ancyrocephalid "Penis" Types.

Studies on the ancyrocephalids of North American fishes started some 50 years ago with the description by Van Cleave and Mueller (1932) of "*Ancyrocephalus aculeatus*" from walleye (*Stizostedion vitreum*: Percidae). Mueller went on to study the parasites of other fishes, including *Lepomis* spp. (Centrarchidae), and between 1934–37 proposed nine genera to accommodate the species he described:

Cleidodiscus 1934	Centrarchids
Urocleidus 1934	Percids
Leptocleidus 1936(a)	Centrarchids
Onchocleidus 1936(a)	
Tetracleidus 1936(a)	
Aristocleidus 1936(b)	
Actinocleidus 1937	
Haplocleidus 1937	
Pterocleidus 1937	

Unfortunately, Mueller's (1934, 1936a, 1936b, 1937) diagnoses and descriptions, based on data from preserved material, were often inadequate and generic separations relied heavily on haptoral features and vaginal characteristics. Mueller attempted to include features of the copulatory apparatus in the generic diagnoses but, with the microscopes available at that time, it must have been almost impossible to study these structures. Both Price (1937) and Mizelle (1938) questioned the validity of several of Mueller's genera and Mizelle and Hughes (1938) soon proposed a sweeping synonymy, only recognizing *Actinocleidus, Cleidodiscus,* and *Urocleidus.* Of these, *Actinocleidus*, with its distinctive orientation of the hamuli, has remained unchallenged but there has been continuing confusion regarding the status of *Cleidodiscus* and *Urocleidus*. According to Mizelle and Hughes (1938), separation of these two genera chiefly depended on the presence or absence of the vagina and whether the accessory piece (if present) was "articulated" with the base of the penis. Both these characters are often difficult to observe, especially in preserved specimens: the vagina, if it is nonsclerotized and submarginal or median, is almost impossible to find unless it contains motile sperm, and the penis/accessory piece attachment can easily be destroyed by subjecting a specimen to excess coverslip pressure.

Price (1967b) reviewed the literature, considered the only feature separating *Cleidodiscus* from *Urocleidus* was presence or absence of the accessory piece/penis articulation, and suggested their possible synonymy. Later, Price and Mura (1969) implemented Price's (1967b) suggestion and declared, on the basis of page priority, that *Urocleidus* was a synonym of *Cleidodiscus*. Prost (1973) was, apparently, not aware of Price and Mura's (1969) paper but considered the structure of the haptor to be the "most essential diagnostic feature" in Monogenean taxonomy and, in agreement with Price (1967b), independently declared *Urocleidus* a synonym of *Cleidodiscus*. Cone (1978) noted some authors have followed Price and Mura (1969) while others have continued to recognize *Urocleidus*.

Bykhovsky (1957) regarded *Urocleidus* as an unnatural collection of species and Suriano and Beverley-Burton (1981) considered it had been used as a "wastepaper basket" for many North American members of the Ancyrocephalidae.

In order to resolve some of the problems concerned with the taxonomy of the North American ancyrocephalid genera, detailed descriptions of type species

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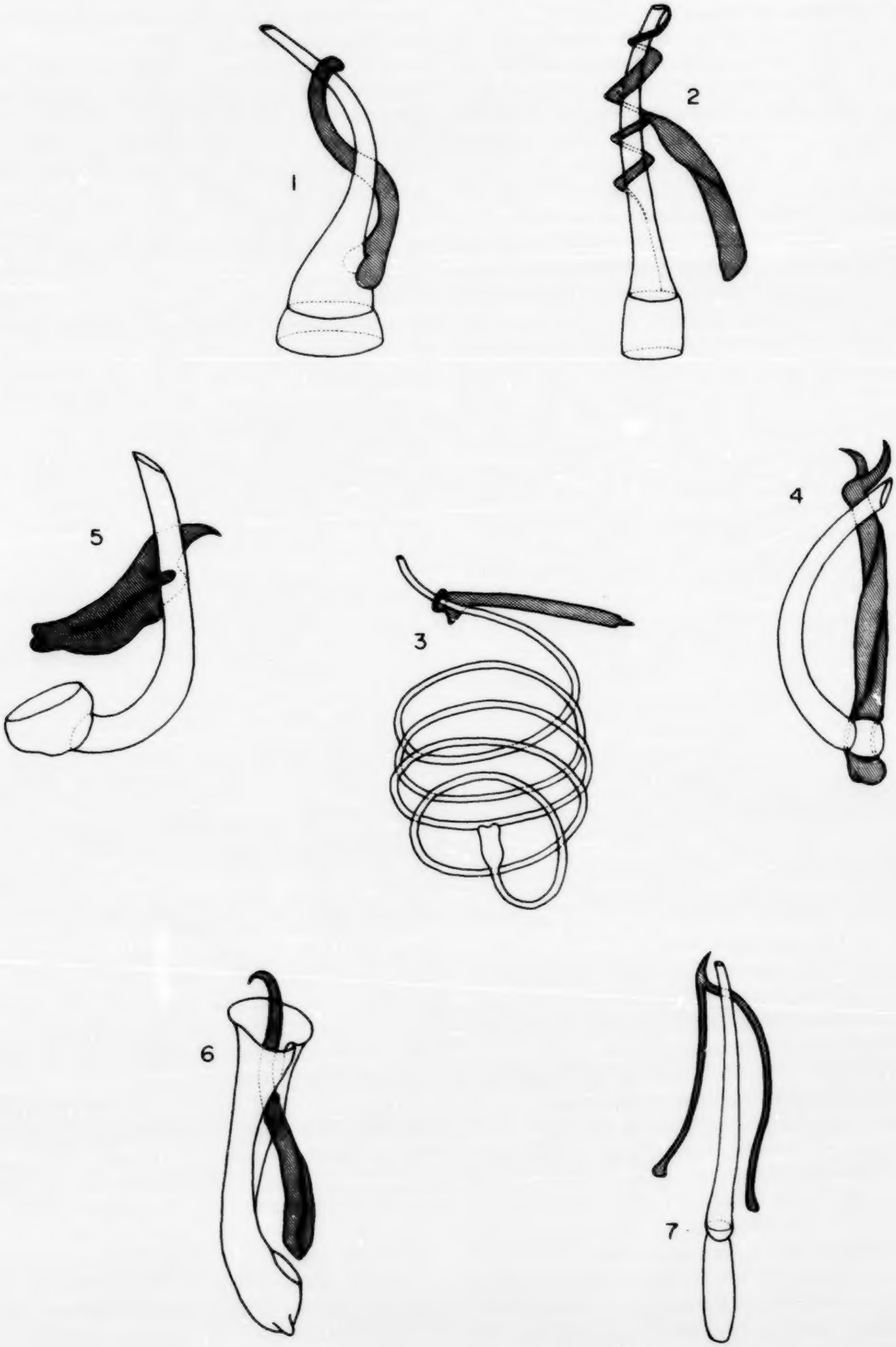
(1)Sensu Llewellyn (1970) not Yamaguti (1963), who regarded the Monocotylidae and Microbothriidae as families within the Capsaloidea.



Appendix 4, Fig. 1–7. "Penis" types from Ancyrocephalidae found in Canadian fishes.

and emended generic diagnoses for several of Mueller's genera have been published in recent years. Thus, *Leptocleidus* (see Sullivan et al. 1978), *Cleidodiscus* (see Beverley-Burton and Suriano 1980a), *Haplocleidus* and *Pterocleidus* (see Beverley-Burton and Suriano 1980b), *Urocleidus* (see Suriano and Beverley-Burton 1981), *Onchocleidus* (see Beverley-Burton and Suriano 1981), *Actinocleidus* (see Beverley-Burton 1981) and *Tetracleidus* (see Murith and Beverley-Burton 1984) are all recognized as valid.

Early in our studies it became evident that several distinct "penis types" exist among the North American ancyrocephalids and that species with a particular penis type usually parasitize a specific host taxon (Suriano and Beverley-Burton 1981, Beverley-Burton and Suriano 1981). Thus, in the present work I have recognized seven different types (listed in alphabetical order) of male copulatory apparatus[1] (penis and accessory piece) as follows (Appendix 4, Fig. 1-7):

Type 1 (Appendix 4, Fig. 1) occurs in *Actinocleidus, Cleidodiscus* and *Lyrodiscus* — parasitic on centrarchids.

Type 2 (Appendix 4, Fig. 2) occurs in *Haplocleidus, Onchocleidus* and *Pterocleidus* — parasitic on centrarchids and *Aethycteron* parasitic on percids (Etheostomatini).

Type 3 (Appendix 4, Fig. 3) occurs in *Leptocleidus* — parasitic on centrarchids.

Type 4 (Appendix 4, Fig. 4) occurs in *Ligictaluridus* — parasitic on ictalurids.

Type 5 (Appendix 4, Fig. 5) occurs in *Salsuginus* — parasitic on cyprinodontids.

Type 6 (Appendix 4, Fig. 6) occurs in *Tetracleidus* — parasitic on centrarchids.

Type 7 (Appendix 4, Fig. 7) occurs in *Urocleidus* — parasitic on percids.

Where more than one genus has a certain penis type (e.g. Type 1), separation is based on differences in the haptoral sclerotizations, e.g., orientation of the hamuli, shape and size of the hamuli and transverse bars, and shape and size of the marginal hooks.

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[1] More detailed descriptions are provided in the diagnoses and keys of the present work and in the relevant research papers.

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